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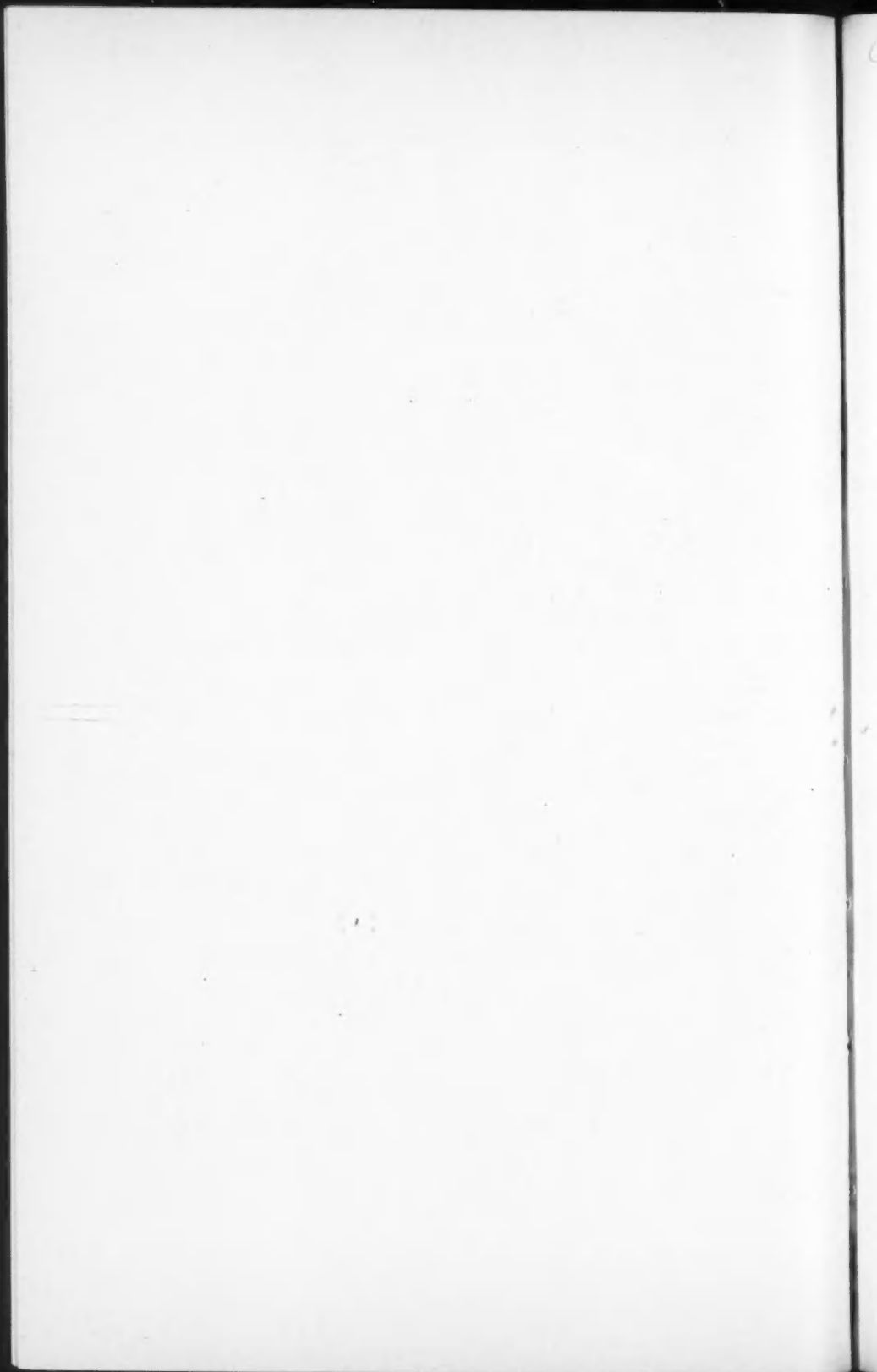
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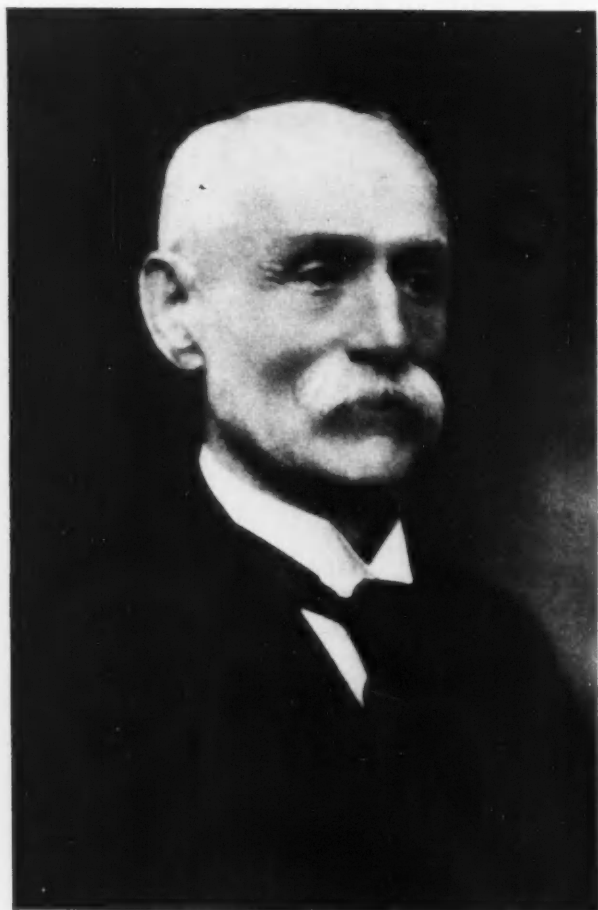
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# OBITUARY

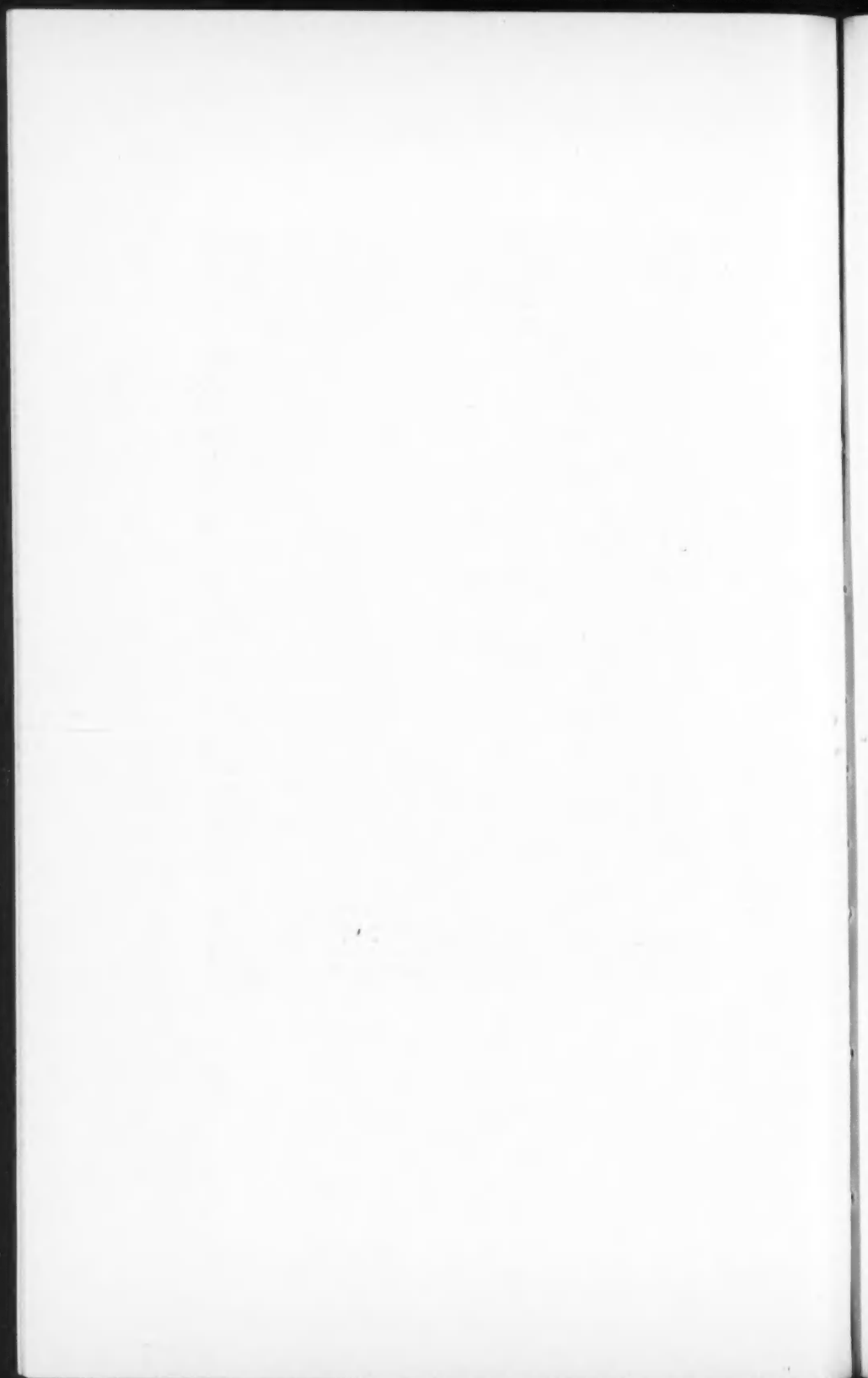


PROFESSOR PHILIP COX, B.A., B.Sc., PH.D.  
1847-1939

Professor Philip Cox, who died on September 12, 1939, at the great age of 92, was a pioneer in the study of the vertebrates, particularly the fishes, of New Brunswick, and was actively connected with both the Natural History Society of New Brunswick and the Miramichi Natural History Association. He was largely responsible for the origin of the latter, which flourished during the period (1897 to 1907) in which he was Principal of the Grammar School at Chatham on the Miramichi river. That amid the exacting duties of teaching and administration he found time for scientific investigation does much to explain his appointment at the age of sixty years to the Professorship of Geology and Natural History in the University of New Brunswick.

Not long after assuming that position he became a volunteer investigator under the Board at the Atlantic Biological Station and even as late as the summer of 1933 he was actively engaged in a study of the mackerel at the Magdalen islands. He was a member of the Biological Board, representing the University of New Brunswick, from 1923 to 1935. Up to the time of his death he remained keenly interested in its work. His ten publications on work done for the Board deal principally with the systematics and general life history of fishes.

Dr. Cox was always enthusiastic and untiring. His great activity on the various investigating expeditions to diverse places on the Atlantic coast from 1917 to 1922 put younger men to shame. As a biological investigator he made noteworthy contributions despite the lack of opportunities and facilities often thought to be necessary.



## Observations on the Viability of *Bacterium salmonicida*

BY D. C. B. DUFF, M. ISOBEL MACARTHUR AND HELEN G. THOMPSON

*Pacific Biological Station*

*and Department of Bacteriology and Preventive Medicine,  
University of British Columbia*

(Received for publication November 15, 1939)

### ABSTRACT

Under laboratory conditions *Bact. salmonicida* multiplies in unaltered domestic sewage and survives therein for 15 days. Removal, destruction or diminution of the original sewage flora resulted in marked multiplication of *B. salmonicida* inocula, and in survival periods of from 13 to 67 days. Viability figures derived from laboratory procedures may not be directly applicable in interpreting the fate of *B. salmonicida* released under natural conditions into natural waters.

### INTRODUCTION

*Bacterium salmonicida* is the etiological agent of furunculosis, a transmissible disease of salmonid and other fresh water fishes. There has been general agreement that *B. salmonicida* survives for only 2 to 3 days in "pure" natural waters and in tap waters (Arkwright 1912, Williamson 1928, Plehn 1911). This finding is supported by unpublished work of our own.

In respect to data on survival in sewage-contaminated water, Plehn (1911, 1924) made use of highly polluted water rendered sterile by passage through a Berkefeld filter. In the menstruum an initial inoculum of 5,800 *B. salmonicida* per ml. had increased at the end of 3 days to 8,803,000 per ml. Williamson (1928), however, records that the organism was not recoverable after one day in unsterilized drain water, and that it existed in scanty numbers only on the third day in sterilized drain water. Horne (1928) records similar short periods of viability for *B. salmonicida* in polluted waters, under the conditions of his experiments.

The investigations recorded below were initiated with a view to obtaining fresh evidence as to survival times in polluted waters.

### METHODS

The experimental containers consisted of 4-litre florence flasks each containing 2 litres of fluid. Samples withdrawn for estimation of bacterial numbers were always at least 1 ml. in volume, and were taken after thorough mixing of the contents of the container. Where necessary, decimal dilutions of such samples were made, and from such dilutions triplicate platings were carried out in most instances. In cases where large numbers of bacteria were present, only those

plates were used for count estimations which contained more than 40 and fewer than 200 colonies per plate (Hill 1908). Inocula consisted of standardized suspensions invariably made from 24-hour agar slant cultures of *B. salmonicida*.

Poured plates were not employed because of difficulty in recognizing sub-surface *B. salmonicida* colonies. Instead, a known volume of sample or of sample dilution (usually 1.0 ml.) was placed in the centre of a previously poured and dried plate of ordinary nutrient agar. By means of a sterile glass spreader, and by rolling, the entire agar surface was uniformly wetted with the inoculum. About 2 hours with tilted lid at 26°C. was allowed for absorption and evaporation before finally inverting the plate. Incubation was carried out at 22°C.  $\pm$  1°. In our hands this plating technique gave excellent results. Anderson and Stuart (1935) have shown the method to be biometrically equivalent, if not superior, to the usual poured-plate technique.

Certain experiments are recorded below in which the behaviour of a *B. salmonicida* inoculum was followed in sewage or sewage dilutions containing all or some of the original sewage microflora. For these series it was found necessary to develop a differential medium in order to distinguish the *B. salmonicida* colonies. Fairly successful results were obtained by the use of a maltose rabbit-blood agar medium,\* which served clearly to differentiate *B. salmonicida* colonies from all but a very few of the normal sewage microorganisms. Where any doubt existed as to the identity of a suspected colony, at a critical point in any experiment, confirmatory tests (morphology, pigment-production, fermentation) were carried out.

All sewage used in these experiments was known to be free from trade and other chemical wastes. The actual "sewage" placed in the experimental flasks consisted of the decanted supernatant fluid from fresh sewage which had stood 2 hours in the laboratory.

## RESULTS

### UNDILUTED FRESH SEWAGE

(a) An initial inoculum of  $350 \pm 50$  *B. salmonicida* per ml. increased in 24 hours to well over 2,000 per ml. In spite of the use of the differential medium, it was difficult in the series to recognize all *B. salmonicida* colonies. The figure of "over 2,000 per ml." is, therefore, a minimum figure based on having picked, from two of the three plates from the 1/1000 sample dilution, two and four colonies respectively, whose identity was subsequently confirmed by morphological and cultural methods. Similarly derived counts of similar magnitude were obtained for 15 days, after which time upgrowth of sewage flora in the experimental vessel rendered further identification impossible.

---

*Prepared peptone-meat-extract agar, pH 7.3 .....	100 ml.
Maltose, C.P. ....	1 g.
Andrade's Indicator. ....	1 ml.
Rabbit blood, sterile, defibrinated or citrated. ....	10 ml.

The maltose is sterilized dry in a thin glass bulb and is later broken into the sterilized medium. The medium is cooled to 45°C. before adding the rabbit blood.



(b) In this experiment the original bacterial content was partly destroyed by heating at 56°C. for 2 hours. The sewage count was thus reduced from 2,750 per ml. to about 130 per ml. The inoculum consisted of  $100 \pm 50$  *B. salmonicida* per ml. Again definite multiplication ensued, with a count of 200,000 *B. salmonicida* per ml. at the end of the 3rd day. Confirmed *B. salmonicida* colonies were recovered up to the 23rd day.

#### UNDILUTED SEWAGE STERILIZED BY BERKEFELD FILTRATION

An initial inoculum of  $100 \pm 50$  *B. salmonicida* per ml. first strongly multiplied, then decreased, the last colony appearing on the 13th day. Experiment terminated on the 17th day (table I).

TABLE I. *B. salmonicida* in Berkefeld-filtered sewage

Day	Bact. per ml.	Day	Bact. per ml.	Day	Bact. per ml.	Day	Bact. per ml.
0	107 116	3	2,450 1,360	6	30 50	10	0 0
1	10,000 10,000	4	5,650 7,240	8	0 2	11	0 0
2	9,120 8,200	5	1,470 2,140	9	1 2	13	1 0

#### AUTOCCLAVED SEWAGE, UNDILUTED (854 mg. organic solids per litre)

Again, with an initial inoculum of  $100 \pm 50$ , definite multiplication was clearly shown. The organism was recovered up to the 22nd day (table II).

TABLE II. *B. salmonicida* in autoclaved sewage

Day	Bact. per ml.	Day	Bact. per ml.	Day	Bact. per ml.	Day	Bact. per ml.	Day	Bact. per ml.
0	82 110	4	9,000 12,800	10	2,000 1,100	15	9 204	20	0 5
1	35,600 36,200	5	5,600 4,500	11	220 190	16	8 4	21	8 2
2	70,800 66,600	6	3,200 2,900	12	58 87	17	0 1	22	1 0
3	16,600 17,400	7	2,900 2,500	14	2 5	19	17 82	23 to 30	0 0

A second experiment gave similar results, except that viable organisms were recovered up to the 35th day.

# AUTOCLAVED SEWAGE, DILUTED (same batch as in No. 3)

Experiments were carried out with varying dilutions of autoclaved sewage supernatant. Figure 1 shows the result of implanting an inoculum of  $350 \pm 50$  *B. salmonicida* per ml. into 2-litre amounts of decimal dilutions of sewage supernatant in tap water. The dilution blanks provided for these series did not carry the dilution of samples to a point high enough to enable determination of the peaks of the curves. Points actually recorded represent the mean of three platings of the particular sample involved. In all cases the numbers of *B. salmonicida*, after having multiplied as shown, remained greatly in excess of 2,000 per ml. for periods of 23 to 29 days, when the numbers again dropped below 2,000 per ml.

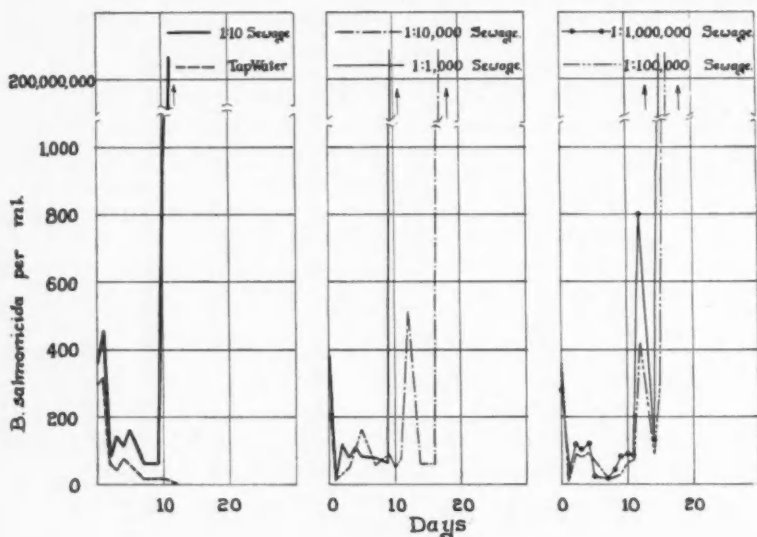


FIGURE 1

The experiment was terminated on the 30th day with a *B. salmonicida* population of over 1,000 per ml. still in existence. The curve for the 1/100 dilution has been omitted from figure 1 for the sake of clarity, since it is closely similar to that of the 1/10 dilution.

## ETHER-TREATED SEWAGE

Following the above observations that the bacillus might fluctuate in numbers over a rather wide range, a further determination was carried out to obtain a numerical record of this behaviour. In this experiment, a portion of the original living sewage microflora was retained alive in the sewage. This result was effected by exposing the sewage to ether vapour as follows. Two litres of the fluid were placed in a 4-litre flask, closed tightly with a rubber stopper. From the stopper was suspended a wide vial containing 30 ml. of ether U.S.P. The flask was shaken

frequently, with care not to spill the liquid ether. When the ether had completely disappeared from the vial, a sterile cotton plug was substituted for the rubber bung. The flask was then allowed to stand at 37°C. until the odour of ether was no longer perceptible. This procedure resulted in the destruction of 60 to 75 per cent of the original microflora. It was found that inocula of *B. salmonicida* in this substrate could readily be followed by means of the differential medium, whereas great difficulty was experienced in obtaining an accurate quantitative picture in sewage containing all its original microflora.

The result of adding an initial inoculum of  $2,000 \pm 200$  *Bacterium salmonicida* per ml. to the treated, undiluted sewage is represented in figure 2. Rapid multiplication of the bacterium occurred throughout the first two days, at the end of

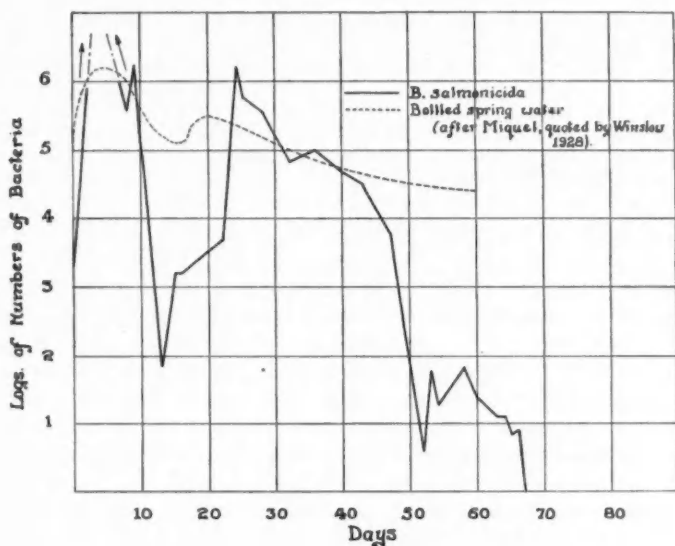


FIGURE 2

which time the numbers amounted to 700,000 per ml., or an increase of 350-fold the original inoculum. Multiplication continued to a still higher degree, as indicated by the presence of *B. salmonicida* colonies in our highest dilutions in such numbers as to be uncountable. The descending limb of the curve was caught on the 7th day at 1,000,000 per ml. A subsequent minor fluctuation was followed by a fairly rapid drop over a period of 6 days, when the count became reduced to the neighbourhood of only 70 per ml. A second sharp rise occurred over the following 9 days, finally followed by a gradual and irregular decrease in numbers over 43 days. The last recovery of *B. salmonicida* occurred on the 67th day after inoculation. During the final gradual decrease, a general increase in the number of native sewage colonies was noted, although counts were not made.

## DISCUSSION

Without reference to the applicability of any of the experiments considered to the interpretation of field conditions, it may be said that our results definitely support and extend the early laboratory findings of Plehn (1911, 1924) as to the ability of *B. salmonicida* to multiply in sewage-polluted waters. The findings are contrary to those of Horne (1928) and Williamson (1928). It is possible that the results of the latter workers have been influenced by the presence of inhibitory trade wastes in the sewage samples employed, since the absence of such agents is not explicitly recorded in their reports. The disagreement may also perhaps be accounted for because of differences in the methods of sampling employed. In figure 1 it is shown that, at least in heat-sterilized sewage of widely varying organic content, the *B. salmonicida* count may drop to a very low figure before extensive multiplication sets in. Some of the lowest counts recorded for the various sewage dilutions were as follows:

Dilution	1/10	1/100	1/1000	1/10,000	1/100,000	1/1,000,000
Lowest counts and day recorded.....	57 (9th)	13 (1st) 30 (5th)	2 (1st) 60 (9th)	2 (1st) 30 (2nd)	2 (1st) 13 (7th)	14 (1st) 11 (7th)

Another relevant situation is demonstrated in figure 2, where extensive primary multiplication is followed by a sharp drop to small numbers on the 13th day followed by a further phase of multiplication. Williamson's samples for plating purposes consisted of loops of fluid and in some cases 0.1 ml. amounts. Horne also sampled by means of the loop. Since there are approximately 75 loopfuls of *B. salmonicida* culture or of average sewage dilution in 1 ml., the employment of such small samples may have led to the non-recovery of the bacterium at a stage where it may have been present in very small numbers.

Reference must finally be made to the applicability of such laboratory results as are recorded here to the interpretation of field conditions. Plehn (1924) has noted that furunculosis is "more destructive" among fish living in polluted waters than amongst those attacked in fresh waters. Her laboratory results show a multiplication of the etiological agent in sewage, so that a causality is at least implied. Whether justification exists for making deductions of this kind seems to us a matter for debate.

It is well known that simply confining a fluid containing a bacterial population in laboratory glassware may lead to a multiplication of the bacteria per unit volume. [Whipple 1901; Winslow 1928 (see figure 2); Waksman and Carey 1935; Zobell and Anderson 1936]. Figure 1 illustrates a peculiar phenomenon in respect to the behaviour of *B. salmonicida* in bottled experiments. If one could consider that the addition of a *B. salmonicida* population to a sterile sewage suspension meant merely the addition of an inoculum to a relatively poor nutrient medium, there would be no need for further explanation. But the curves indicate that very similar multiplication occurs in widely varying dilutions of the sewage, that

is in widely varying concentrations of nutrient. The close similarity of the curves for dilutions 1/10,000 to 1/1,000,000 suggests that dilution of nutrient is not at all a major factor, although obviously when nutrient is completely eliminated (as in the tap water control), no multiplication is possible. It is, therefore, possible that some of the multiplication of the pathogen in these experiments may be attributable to the confinement of its menstroom in laboratory glassware. Should this be the case, such findings might have no direct bearing whatever on the behaviour of the pathogen under field conditions in which the organism is released into a practically infinite volume of fluid. It would seem a point worthy of further investigation that a non-indigenous pathogen may under certain conditions react to bottling in a manner similar to indigenous saprophytic bacteria.

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## Growth of Young Shipworms (*Teredo navalis*) in Malpeque Bay

BY A. W. H. NEEDLER AND A. B. NEEDLER  
*Prince Edward Island Biological Station*

(Received for publication January 9, 1940)

### ABSTRACT

In spruce boards from July 6 to November 12 growth was as much as 24 cm. with, and 5 cm. across, the grain; fastest at high temperatures but continued even below 10°C.

On the Canadian Atlantic coast the shipworm, *Teredo navalis* L., is common (M'Gonigle 1925) in the warm waters of the southern part of the gulf of St. Lawrence. There both salinities and temperatures are favourable in inlets such as Malpeque bay. In this region, at the northern limit of its range, it is one of an isolated warm water community including such forms as oysters (*Ostrea virginica*), quahaugs (*Venus mercenaria*) and many others. It is of some interest to determine its rate of growth in this situation.

As attack by shipworms is a serious menace to wooden equipment used in oyster culture in these waters, it has been the subject of investigation at the Prince Edward Island Biological Station. In this connection interest is centred in the prevention of damage to light movable equipment exposed for only part of the year, which presents problems quite different from those involved in the protection of permanent structures. Knowledge of the season when *Teredo* larvae settle is important for avoiding or protecting against the worst danger. Surface protection can be used as it can be renewed on movable equipment. The rate of growth during a single season is important as it determines what damage may be expected from small gaps in surface protection. A heavy attack on unprotected wood, amounting at times to over one hundred individuals per square cm., would be serious even with very slow growth, but the rate of growth governs the damage when the shipworms are not crowded in the wood, as in a light general attack or a heavy one through small unprotected areas.

### METHODS

Planed spruce boards, 36 inches (91.4 cm.) by 3 inches by  $\frac{3}{4}$  inch, were painted with two coats of copper paint except for a patch  $\frac{1}{4}$  inch square on one side near the lower end. These were placed in the water at the landing stage of the Biological Station on July 6, so as to be covered at all times, with the lower end closer to the bottom than the surface. Each fortnight until November 12 one was removed and later examined by carefully chipping away the wood.

## RESULTS

As *Teredo* larvae settled on the boards immediately it may be assumed that most of the largest shipworms in each board had entered the wood within a few days of July 6. As from about twenty to about fifty shipworms entered the small unprotected patch, crowding at the point of entry was unavoidable, but within the wood there was adequate room for the maximum growth of a number of individuals.

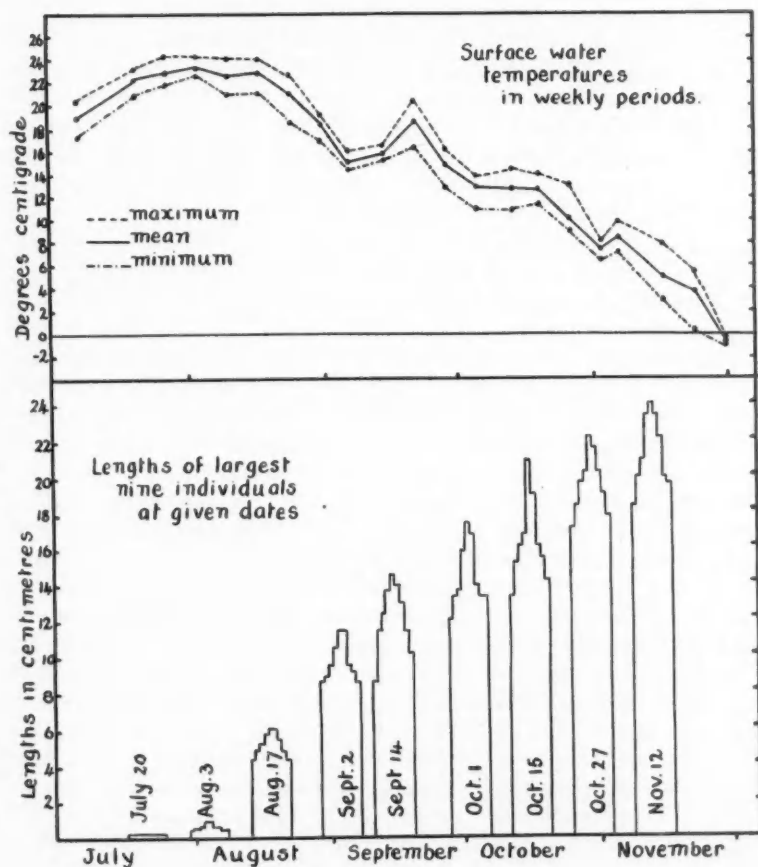


FIGURE 1. Lengths of the largest nine shipworms in the test boards, and water temperatures throughout the experiment.

The length of the shipworms when the boards were removed varied greatly, probably due in part to the different times at which the larvae entered the wood. Some of the individuals, however, seem to have been badly crowded in the wood. The shipworms radiated from the unprotected patch, but there was a tendency

to grow with the grain as soon as crowding permitted. Some individuals reached the opposite side of the board but hardly any reached the edges. As the length of all the individuals could not be measured and as some of the smallest entered the board some time after July 6, the lengths of only the largest were determined. Figure 1 shows the lengths of the largest nine in each board as well as the water temperatures.

As the number of shipworms in the individual boards varied, the largest nine includes a higher proportion and relatively smaller sizes in some boards than in others. This must be remembered in interpreting the results.

The figure shows a regular progression in the maximum lengths of the individuals as the season advanced. This was closely paralleled by the average length of the largest nine individuals. The absolute rate of growth was at first small, fastest in the late summer and tending to slow down slightly late in the autumn. Although the growth is not shown very accurately by this method, the data indicate that the most rapid growth occurred when temperatures were high but that some growth continued after the temperature had fallen below 10°C.

As the temperature fell below 0°C. shortly after the experiment was terminated, it is believed that almost the entire season's growth is shown. This indicates the maximum damage effected by the shipworms in a single season in lumber of this kind, since the boards were exposed within a few days of the first settlement of *Teredo* larvae in that year. It is shown that even a small fault in surface protection may cause weakening of the wood as far as 24 cm. This maximum distance is, however, likely to occur only in the direction of the grain as the experiment indicated that hardly any individuals reached the edges of the boards which were only about 4 cm. from the unprotected patch.

The salinities throughout the experiment were between 26½ and 29 per mille, with irregular fluctuations from day to day. The experiment does not serve to indicate any effect of salinity on the rate of growth.

Spruce boards were used in the experiment because this is the type of lumber most commonly used for wooden oyster culture equipment. From other observations it is evident there is a general tendency for the rate of growth to be slower in harder woods. As an extreme case may be mentioned boards of greenheart in which, after exposure for a full season, the numerous living *Teredo* were only about 3 mm. long.

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# The Development of the Vertebral Column of the Pacific Herring (*Clupea pallasii*)

BY AGNES M. GWYN  
University of British Columbia  
and  
Pacific Biological Station

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## ABSTRACT

Embryological development is followed over a period of ten weeks after hatching. The mode of formation of the components of the vertebral column is compared with that in *Clupea harengus*, and is described in detail where differences are observed or additional information is available. Development appears essentially similar in the two species, although in general more rapid relative to length in *C. pallasii*. At hatching, myotome formation is complete and the ultimate vertebral number of an individual is presumably determined by that time. During ossification of the vertebral column, complex growth gradients from one or more centres are observed.

Vertebral number is a widely used character in the racial study of fishes. Recently it has been found that change in vertebral number can be related to the temperature of the water during the early stages of development (Rounsefell and Dahlgren 1932; Tester 1938). From this knowledge has arisen the question of the time at which the component parts of the vertebral column are formed and development completed to the point beyond which there can be no change in the fundamental structure. An attempt has been made, therefore, to trace the steps in development from the time at which the young fish are first hatched until development is more or less completed.

Developmental study of the vertebral column of teleostean fishes has occupied the attention of many workers. Until recently, however, investigations have been restricted to species with relatively large eggs and shortened larval and post-larval stages. Ramanujam (1929) has made a very important addition to this series of papers with his study of the vertebral column in the Atlantic herring (*Clupea harengus*), which has a short egg stage and a relatively long developmental period, and he has covered very completely the embryology and histology of the various parts of the vertebrae. The present author, in working with the Pacific herring (*C. pallasii*), has related this phase of the work directly to that done by Ramanujam, since the fundamentals of development appear to be similar in the two species.

## ACKNOWLEDGMENTS

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Fraser and Professor G. J. Spencer of the University, under whose supervision the work was done, for advice and assistance; to Dr. W. A. Clemens, Director of the Pacific Biological Station of the Fisheries Research Board of Canada, for making the initial arrangements for the research and for providing the facilities at the Station; to Dr. J. L. Hare, for helpful criticisms of the manuscript. Grateful acknowledgments are made to Dr. A. L. Tester, Pacific Biological Station, at whose suggestion this problem was undertaken, for providing the material, suggesting methods of attack, and for his invaluable assistance in preparing the paper for publication, and to Mr. J. L. McHugh, who very generously supplied a sample of young herring and who gave access to data on the early growth rate. Permission to publish this paper has been granted by the Department of Zoology, University of British Columbia.

#### MATERIAL

This consists of larvae and post-larvae taken on the southeast coast of Vancouver island, British Columbia. Early samples (under 20 mm. in average length) were taken in tow nets and later ones by dip net. In Nanoose bay in 1932 samples were taken on various dates with average lengths in mm. as follows: March 11, embryonic, less than 7; March 19, 7.8; March 24, 9.3; April 5, 11.1; April 13, 11.7; April 21, 12.7; April 26, 14.3; May 2, 15.7; May 9, 21.4; May 16, 28.3; and May 26, 34.5. In or near Departure bay in 1932 samples were taken on dates and with lengths as follows: April 1, 8.4; April 11, 7.2; April 12, 7.6; April 25, 13.3; May 28, 39.3; June 2, 33.8; June 6, 38.3; and June 21, 39.4. In Departure bay in 1939 a sample was taken on May 17 with a length of 30.1 mm.

In the series from Nanoose bay, spawning took place in the first week in March and hatching began on March 17. Spawning probably took place about three days earlier at the head and west shore of the bay than at the entrance. Fish from both spawnings may well appear in the same sample.

That the 1932 Departure bay series does not run uniformly, may be attributed to there being several different spawnings in that bay. The 1939 sample was the product of hatchings on March 22 and 28.

For 1932, average lengths are based on total lengths of 10 specimens for each sample. For 1939, the entire sample of 151 was measured from snout to caudal peduncle, and the result converted into total length with a factor determined by measuring 100 fish by both methods.

Figure 1 shows the growth in length of the Nanoose bay fish, the curve departing radically from a straight line. The apparent slowing of growth rate between the second and eighth weeks, with rapid increase subsequently, is thought to be due to selective sampling. If the larger fish tend to school (as seems to be the case), samples taken with tow nets will consist only of the smaller fish. Further, even when the dip net is used on fish in schools, smaller individuals may escape through the meshes. Therefore, combination of these two factors of selection, probably coupled with the presence of larvae from successive spawnings, may well account for the shape of the curve. Some such explanation seems necessary, since recent work by Mr. J. L. McHugh of the Pacific Biological

Station indicates that the growth in length of herring from hatching to the eighth week approximates a straight line.

Preservation of the material in 5 to 10 per cent formalin unfortunately resulted in destruction of the more delicate tissues, but bone and cartilage were not noticeably affected for histological study.

#### METHODS

Longitudinal sections of all stages and transverse sections of stages up to that of May 9 were cut at  $10\mu$  after embedding in paraffin in the usual way.

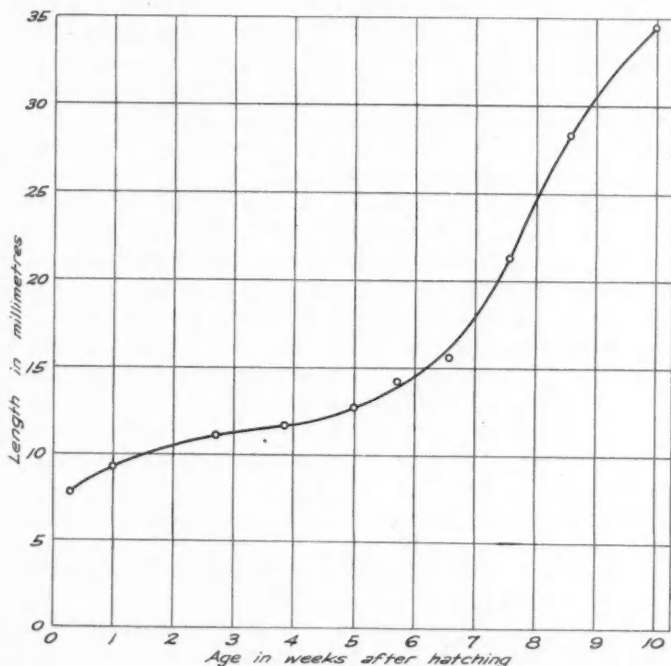


FIGURE 1. Growth in length of herring larvae and post-larvae from Nanoose bay, 1932.

Decalcification was not necessary. Larger sections were held on slides by means of a collodion solution. Mallory's triple stain was found to be the most satisfactory of several that were used and was specific for bone (dark blue) and cartilage (light blue).

For studying somite formation, advanced embryos and newly-hatched larvae were stained *in toto* in borax carmine and alum cochineal, and were cleared in cedar oil before examination under low-power microscope. Some of these preparations were embedded and sectioned.

For studying bone formation, advanced larvae and post-larvae were cleared

in potassium hydroxide and stained with Alizarin Red S. The use of a 1 per cent clearing solution over a period of several weeks gave better results than the use of a 4 per cent solution over a shorter interval.

#### STAGES OF DEVELOPMENT

In cleared whole mounts of embryonic specimens (less than 7 mm.) taken approximately 8 days before hatching, somite formation is visible in the thoracic and abdominal but not in the caudal region of the body. From studies of the Atlantic herring at this stage (Ramanujam 1929) it may be assumed that the more anterior somites have already differentiated into myotome and sclerotome.

At or immediately following hatching (7.8 mm.), there is reason to believe that myotomic formation is complete. Although the myotomes in the caudal region cannot be seen in cleared whole mounts, they may be traced in longitudinal sections to a point at which they become reduced to a narrow band of muscle and at which there is a relatively large amount of sclerotome lying on either side of the notochord (fig. 2a). This is considered to be the point of differentiation of the future tail skeleton from the vertebral column proper. Anteriorly the sclerotome forms a very thin layer of tissue which may only be seen in the intermyotomic regions. The elastica externa is not differentiated from the epithelial layer of the notochord (fig. 4b). Within the notochord, the septa are very numerous and are not directly related to the myotomes as there are three or four to each one. At a comparable stage in the Atlantic herring, the elastica externa could be distinguished and the sclerotome formed a continuous layer around the notochord (Ramanujam 1929). The absence of this continuous layer in the present material may be the result of its poor state of preservation.

At 9.4 mm., about five days after hatching, the elastica externa can be distinguished as a band of dense wavy fibres lying in close contact with the epithelial layer of the notochord (fig. 4b). Precartilaginous cells may be seen in the caudal region of the body. These latter were reported in the Atlantic herring at the time of hatching.

At 11.1 mm., several of the hypurals have formed in hyaline cartilage (fig. 2b). At 11.7 mm. the posterior haemal arches are indicated by massing of the skeletogenous cells in the intermyotomic spaces. In both these latter stages a thickening in the ventral wall of the notochordal sheath may represent the ventral longitudinal ligament. At 12.7 mm. the elastica externa is separated from the epithelium of the notochord by a lightly staining layer of fine fibrils running concentrically, the inner fibrous sheath or elastica interna (fig. 4c). At this time, also, the perichordal sheath can be seen for the first time completely surrounding the notochord. At one point in the caudal region there is apparent invasion of the notochordal sheath by cartilaginous nuclei from the skeletogenous layer. Four (II-V) anterior hypurals are present in hyaline cartilage (figs. 2c and 3b). By the next stage (14.3 mm.) the epithelial layer of the notochord has become more distinct and widened triangles of tissue are present at the bases of the septa, each with a single nucleus (fig. 4d). The tail structure is completed in hyaline cartilage, and, within a week (15.7 mm.), the tail is flexed dorsally as in the final structure (fig. 2d).

In the Atlantic herring, the majority of these advances in development are described in the 16 mm. stage. At this time the fibrous layer of the notochord

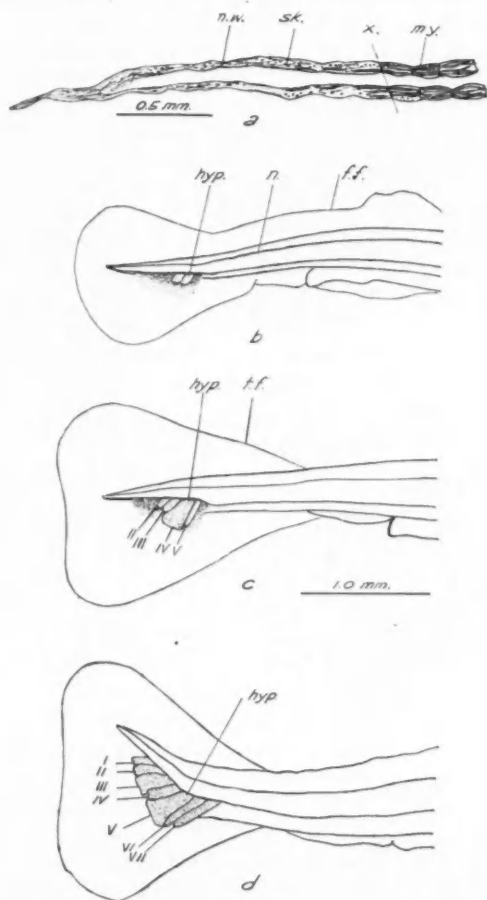


FIGURE 2. Development of the caudal skeleton. Sagittal section: a,—(7.8 mm.), whole mounts: b,—(11.1 mm.); c,—(12.7 mm.); d,—(15.7 mm.). (*f.f.*, fin-fold; *hyp.*, hypurals (as numbered); *my.*, myotome; *n.*, notochord; *n.w.*, notochordal wall; *sk.*, sclerotome; *t.f.*, tail-fin; *X*, probable position of the end of the vertebral column).

is present, and there are median thickenings of the dorsal and ventral walls of the notochord representing the dorsal and ventral longitudinal ligaments respectively. All the hypurals are represented.

At 21.4 mm. in the Pacific herring, alizarin-stained specimens show the formation of a single bony ring of the vertebral column (fig. 5a). This lies in juxtaposition to the base of the third hypural and is the third of the three bony

rings which form posterior to the penultimate centrum, making up the urostyle. The uroneurals of the penultimate centrum are also present. In contrast to the remainder of the extracentral structures these are not preformed in cartilage. The perichondrium of the hypurals has become ossified. The more posterior neural and haemal arches are present in hyaline cartilage (fig. 3c).

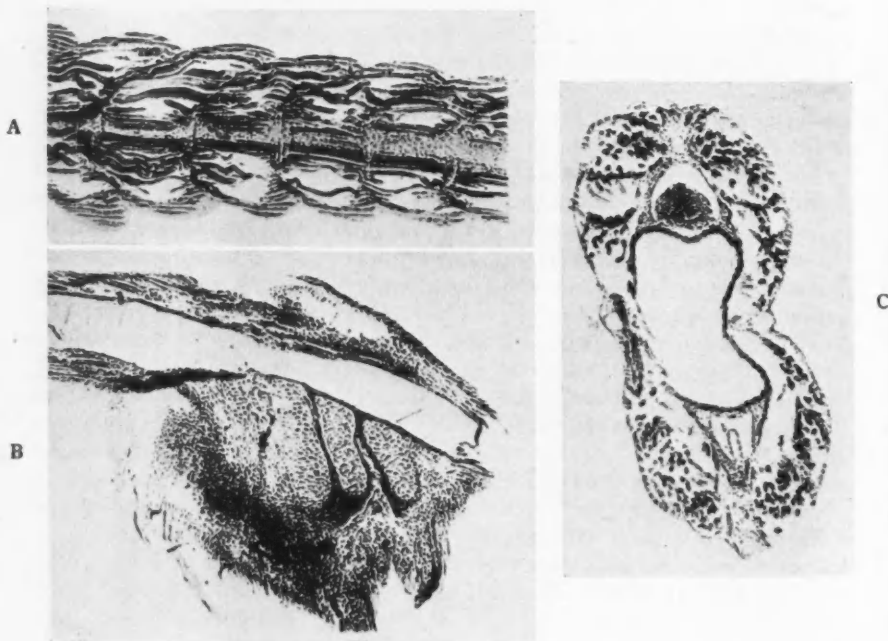


FIGURE 3. A, 14.3 mm. (Nanoose bay). Sagittal section through the caudal region lateral to the notochord. Skeletogenous cells of the perichordal sheath showing the anlage of the vertebrae in relation to the myotomes. Photomicrograph on panchromatic plate with red filter (x 75). B, 14.3' mm. (Nanoose bay). Sagittal section through the notochord in the region of the hypurals; 6th, 5th, and 4th hypurals of hyaline cartilage indicated. Photomicrograph on panchromatic plate with red filter (x 75). C, 21.4 mm. (Nanoose bay). Transverse section in the caudal region. Neural and haemal arch of hyaline cartilage lying in contact with the notochord. Photomicrograph on panchromatic plate with red filter (x 75).

Within a week (28.3 mm.), the entire notochord has become converted into vertebral and intervertebral regions (fig. 5b). In the vertebral regions, the elastica externa has been modified to form the inner bony rings of the centra, and both the epithelium and the perichordal sheath are loosely formed with elongated nuclei. In the inter-vertebral regions, the elastica externa is undifferentiated, the interna is very much thickened and pushed up between the ends of the bony rings (fig. 4e) and both the epithelium and the perichordal sheath are thickened

and the cells contain rounded nuclei. The perichondrium of a large number of the arches and of the more posterior spines has become ossified, though there is still a considerable amount of cartilage to be seen in sections of the bases of the arches (fig. 5e). The basidorsals and basiventrals lie in close contact with the inner bony rings of the centra and are placed at the cranial ends. Anteriorly these cartilages project over the cranial ends and lie almost intervertebrally. Although Ramanujam describes intercalaries in connection with the basidorsals of the first two vertebrae, these were not found in the present material and the author is inclined to agree with Farugi (1935), who suggests that their apparent presence is due to oblique sectioning of the arch cartilages.

Fish of the 1939 Departure bay sample, with a length range of 21 to 36 mm. and of an age comparable to the latter two stages of the 1932 Nanoose bay series, show the order of appearance of the inner bony rings of the centra. Almost immediately after the appearance of the posterior (third) bony ring of the urostyle, formation begins in the abdominal region. In some specimens there are narrow bands of bone constituting the inner rings of the 9th to the 27th centrum. In others the bony rings are present from the 3rd to the 4th centrum and, in a few, the second ring of the urostyle is formed. In still more advanced specimens, the bony rings are present from the 1st to the 44th centrum, with development continuing in a caudad direction. At the time of formation of the 47th centrum, the ventral portions only of the last five true vertebrae are formed, whereas the newly-developed penultimate centrum is entire. The second bony ring of the urostyle may either be complete or formed only ventrally. Completion of these bony rings takes place at a length ranging from 25 to 28 mm. In most cases the last to form is the one posterior to the penultimate centrum. It might be stressed that although the ventral portion of the more posterior vertebrae very definitely develops in advance of the remainder of the ring, this same gradation could not be distinguished in any other region of the body.

In both the 1932 Nanoose bay and the 1939 Departure bay fish, bone is first present in the tail region at approximately the same average length (21 mm.). In the former, the inner bony rings of the centra are formed along the entire vertebral column at an average length of 28.2 mm. (range: 23 to 33 mm.), and in the latter at an average length of 28.5 mm. (range: 21 to 33 mm.). In the Atlantic herring the early appearance of the third bony ring of the urostyle is not described, and presumably did not take place in the 20 to 30 mm. stage. The inner rings were present over the entire column at the 30 to 40 mm. stage, i.e., general ossification took place at lengths which were, on the average, considerably greater than in the Pacific species.

At 34.5 mm. (Nanoose bay, 1932 series), a second layer of bone is formed in the vertebral regions (fig. 5c). This outer ring is true membrane bone, formed by direct ossification of the perichordal sheath in concentric rings. These outer rings entirely surround the inner rings, but are broken in the regions of the arcualia. Posteriorly, small projections, the zygapophyses, arise dorsally and ventrally on either side of the centra, and are also formed from the perichordal sheath. All of the arches are now surrounded by perichondrial bone. A small projection, corresponding to the anterior zygapophysis of higher vertebrates,



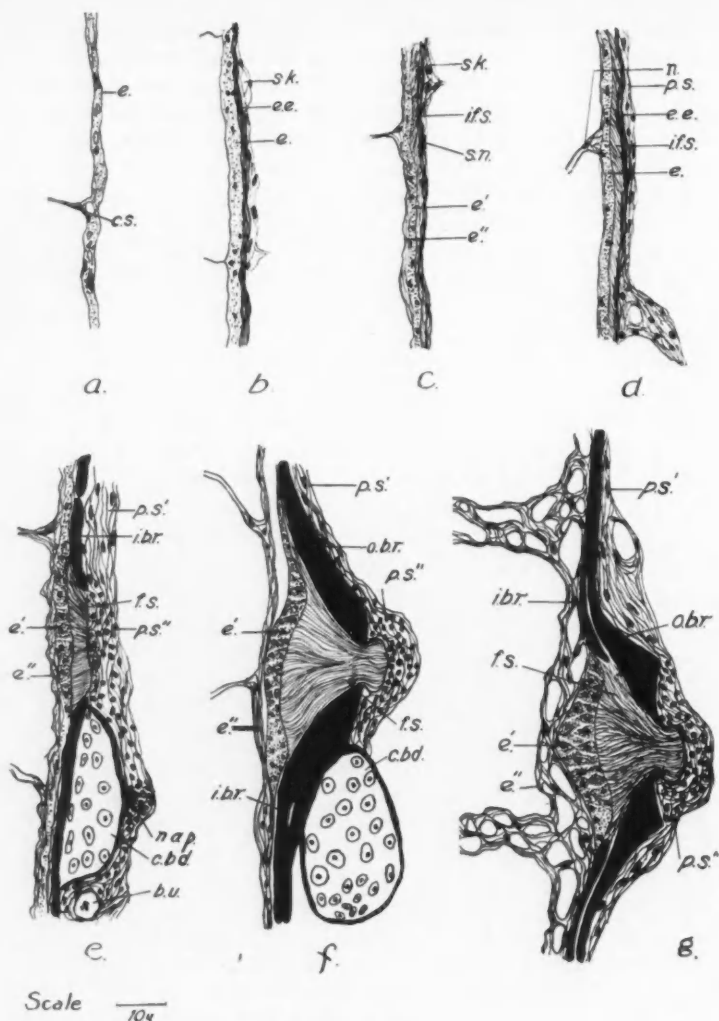


FIGURE 4. Sagittal sections of the notochordal wall, showing steps in development. From Nanoose bay: a,—(7.8 mm.); b,—(9.4 mm.); c,—12.7 mm.); d,—(14.3 mm.); e,—(28.3 mm.); f,—(34.5 mm.). From Departure bay: g,—(39.4 mm.). (b.v., blood vessel; c.b.d., cartilaginous basidorsal; c.s., chordal septum; e., epithelium of the notochord; e', nucleated layer of the epithelium; e'', slightly vacuolated layer of the epithelium; e.e., outer fibrous sheath (elastica externa); f.s., fibrous sheath of the notochordal wall; i.f.s., inner fibrous sheath; i.b.r., inner bony ring of the centrum; n., nucleus at base of septum; n.p., neuropophysis; o.b.r., outer bony ring of the centrum; p.s., perichordal sheath; p.s', perichordal sheath in the vertebral regions; p.s'', perichordal sheath in the intervertebral regions; s.k., sclerotome; s.n., skeletogenous nucleus which has invaded the externa)



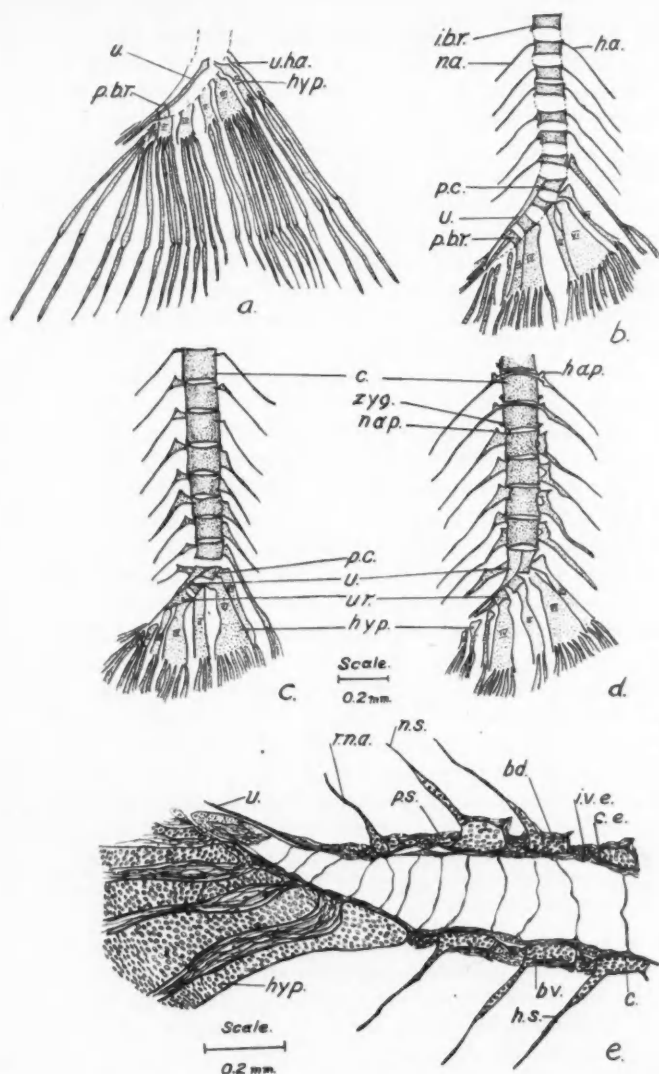


FIGURE 5. Development of the caudal region of the vertebral column. Stained cleared specimens. From Nanoose bay: a,—(21.4 mm.); b,—(28.3 mm.); c,—(34.5 mm.). From Departure bay: d,—(33.8 mm.). Sagittal section. From Nanoose bay: e,—(28.3 mm.). (*bd.*, basidorsal; *bv.*, basiventral; *c.*, centrum; *c.e.*, chordal epithelium; *h.a.*, haemal arch; *hap.*, haemapophosis; *h.s.*, haemal spine; *hyp.*, hypural; *i.b.r.*, inner bony ring of the centrum; *i.v.e.*, intervertebral enlargement; *nap.*, neurapophosis; *n.a.*, neural arch; *n.s.*, neural spine; *p.b.r.*, posterior bony ring; *p.c.*, penultimate centrum; *p.s.*, perichordal sheath; *r.n.a.*, rudimentary neural arch in conjunction with the penultimate centrum; *u.*, uroneural; *ur.*, urostyle, with the two posterior bony rings now fused; *zyg.*, zygapophysis)

arises from just above the base of each arm of the arches. The structure of the arches varies in different regions of the body and is fully described by Ramanujam (1929). At this stage also, the fibrous sheath in the intervertebral regions is very much thickened and pushed up between the tips of the centra. The intervertebral regions of the epithelial layer are marked by columnar cells with rounded nuclei. The inner layer of the epithelium, which is continuous throughout the length of the chord and to which the septa are attached, is becoming vacuolate (fig. 4f). Fine intermuscular bones formed by ossification of the connective tissue between the muscle layers project dorso-laterally and ventro-laterally from the basidorsals and basiventrals respectively.

In the Atlantic herring, formation of the outer bony rings and intermuscular bones takes place at about the 45 mm. stage. Vacuolation of the inner epithelial layer of the notochord is described at 50 mm., when longitudinal as well as transverse septa were observed.

In the latest stage available, 39.4 mm. (Departure bay, 1932), development consists largely of the thickening of the centra by concentric ossification of the perichordal sheath. The rims of the centra show relatively greater increase in thickness, and have grown over the intervertebral enlargements of the fibrous sheath. Zygapophyses are present on all centra of some specimens (fig. 5d). The epithelial layer of the notochord shows considerable development: the inner layer is extremely vacuolate with the vacuoles extending into the septa, and elongated nuclei are present throughout (fig. 4g). The posterior tip of the notochord is filled with vacuolate cells and is surrounded only by the fibrous sheath, in which state it remains in the adult fish. Bone-forming cells are invading the hypurals at the free end. The uroneural is fused with small projections homologous to it, which arise from the three posterior bony rings.

All the fundamental structures are now present. With subsequent thickening of the centra, fusion of the urostylar elements, and continued modification of the epithelial layer and fibrous sheath of the notochord, the adult vertebral column is attained.

#### SUMMARY AND DISCUSSION

Steps in the development of the vertebral column may be briefly summarized as follows:

At the time of hatching (7 to 8 mm.), myotomic formation is complete. Massing of the skeletogenous cells on the ventral side of the notochord in the posterior region takes place within the next four or five days, and marks the region of the tail cartilages. Within three weeks (12 mm.), precartilaginous cells form the anlage of the hypurals and the more posterior arches of the vertebral column proper. By the seventh week (16 mm.), the more anterior arches are similarly indicated and those posteriorly have now developed cartilage cells. The seven hypurals are also completed in hyaline cartilage and the tail is flexed dorsally. At about the end of the eighth week (21 mm.), a single bony ring appears adjacent to the base of the third hypural. This is the most posterior of three centra which develop behind the penultimate. By the ninth week (28 mm.), bone is formed

in the vertebral regions over the entire length from the basiocciput to the end of the urostyle. Cartilaginous arches are present all along the vertebral column. The outer bony rings of the centra are laid down in the tenth week (34 mm.), and apart from the fusion of the urostyle and the subsequent thickening of the centra the vertebral column is complete.

With the exception of the first and last two, the age-length relations given in the above summary cannot be considered as representative of the herring population as a whole, because of the possibilities of selective sampling.

As myotomic formation, as far as can be determined, is complete in newly-hatched larvae, and as the myotomes correspond directly with the vertebrae (fig. 3A), there being no division of the somite into cranial and caudal regions, it seems reasonable to conclude that the ultimate vertebral number of an individual has already been established at the time of hatching.

It may be stated that, in general, for a given length the Pacific herring is at a more advanced stage of development than the Atlantic herring. Since time after hatching is not given for the latter, age comparison cannot be made. One apparent exception to this observation involves the perichordal sheath. Ramanujam has noted a complete sheath just after hatching; in the present case the complete sheath could not be distinguished until two or three weeks after hatching, but this may have been due to poorly preserved material. Another exception lies in the fact that the elastica externa was clearly distinguished at the time of hatching in the Atlantic herring but not until a week after hatching in the Pacific species.

The fundamentals of development appear to be similar in the Atlantic and Pacific herring. It might be noted, however, that the dorsal longitudinal ligament, described in the former, was not apparent in the latter. The present study supports Ramanujam's (1929) conclusion regarding the presence of three distinct types of bone in the vertebrae, and also his conclusion that the herring is transitional between the elasmobranchs and the osseous Ganoids and Teleosts, in that the inner bony rings are formed by direct ossification of the notochordal sheath with but a small degree of invasion of cartilaginous cells from the skeletogenous layer.

Attention is called to various growth gradients which have been encountered. The hypurals, the first precartilaginous structures to appear, develop on the whole from the anterior to the posterior end, but possibly not in regular order. Both neural and haemal arches, on the other hand, start to develop anteriorly from a point adjacent to the penultimate centrum. A short time later they begin to form in the segments just posterior to the head and development proceeds posteriorly. Thus the arches are formed last in the abdominal region. In contrast to the arches, the inner bony rings of the centra of the true vertebrae form first in the abdominal region and development proceeds in regular order both anteriorly and posteriorly. Whether growth starts from a single centre, or whether several of the bony rings are laid down simultaneously, cannot be stated definitely. A marked ventro-dorsal growth gradient is apparent in the formation of the inner bony rings of the last five true vertebrae, the penultimate centrum and the 1st and 2nd rings of the urostyle. Although the third ring of the urostyle

is the first bone to be laid down in the vertebral column, subsequent formation of inner bony rings of the urostyle and penultimate centrum does not proceed regularly. The penultimate centrum is entire at approximately the same time as the 47th centrum.

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## The Distribution of Pteropods in the Waters of Eastern Canada and Newfoundland

By C. J. KERSWILL

*Biological Department, University of Toronto*

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### ABSTRACT

Pteropod collections from several expeditions show both *Clione limacina* and *Limacina helicina* in the arctic, Hudson bay and strait, southward to cape Sable, and in the gulf of St. Lawrence, with *L. helicina* generally more abundant except at the south. *L. retroversa*, absent in northern collections, was more abundant than the other species from Belle Isle strait to cape Sable, increasing in numbers in the gulf of St. Lawrence in summer.

Three species of pteropods (for descriptions and figures see Sars 1878) have occurred in the collections made on several Canadian Government expeditions, *Clione limacina* Phipps, *Limacina helicina* Phipps, and *Limacina retroversa* Fleming (Pelseneer 1888, Bigelow 1928, and Johnson 1934; but *Spiralis balea* of Sars 1878).

All were widely distributed in the plankton hauls made during the Canadian Fisheries Expedition of 1914-1915 and the Biological Board's Belle Isle Strait Expedition of 1923 in waters from cape Sable to Belle Isle strait. *C. limacina* and *L. helicina* occur in shore collections made in 1927 by Mr. Frits Johansen and in 1928 by Mr. B. W. Taylor, who were sent by the Biological Board to accompany expeditions of the Department of Marine and Fisheries in Hudson strait, and in plankton hauls taken on the Hudson Bay Fisheries Expedition of 1930, with Mr. H. B. Hachey of the staff of the Biological Board as officer-in-charge. The opportunity of working over the pteropod material obtained on these expeditions has been very kindly afforded the writer by Dr. A. G. Huntsman at the University of Toronto.

Shore collections of pteropods and observations on their occurrence have been made by several zoologists who have accompanied the R.M.S. "*Nascopie*" on the Eastern Arctic Patrol, namely Mr. H. M. Rogers in 1937, Mr. T. M. Shortt of the Royal Ontario Museum of Zoology in 1938, and Mr. J. G. Oughton of the Royal Ontario Museum of Zoology in 1939. These persons have kindly granted the writer permission to examine the pteropods which are now in the Royal Ontario Museum of Zoology, and to publish the records of their occurrence.

## SOUTHERN REGION

The collections in the southern region from cape Sable to Belle Isle strait were made with standard plankton nets, permitting a quantitative treatment of the combined data.

During the Canadian Fisheries Expedition of 1914-1915, plankton hauls were made on spring and summer cruises of the C.G.S. "*Acadia*" off the coasts of Nova Scotia and Newfoundland, on spring and summer cruises of the C.G.S. "*Princess*" in the gulf of St. Lawrence and by the steam drifter "*No. 33*" between Anticosti and Gaspé in August. Three kinds of hauls were made with a No. 0 net of bolting cloth, (1) vertical hauls, (2) vertical closing hauls, and (3) tow hauls. The pteropods taken on this expedition were identified and counted by Dr. A. G. Huntsman, who has kindly made his records available to the writer. While some "Gulf Stream" species of pteropods have occurred at outer stations visited by the C.G.S. "*Acadia*", only the three species which have occurred commonly over the whole region are considered here.

On the Belle Isle Strait Expedition of 1923 hauls of the same kind were made in August and September by the C.G.S. "*Arleux*" and the motorboat "*Prince*" at stations in Esquiman channel, Belle Isle strait, off the coast of Labrador and Newfoundland, and across Cabot strait. The pteropods taken on this expedition and preserved in formalin have been identified and counted by the writer. These data have been supplemented in several instances by the plankton records made by Dr. Huntsman where swarms of pteropods occurred and estimates of their numbers were made but no specimens were preserved.

The data for the horizontal distribution of each species are shown graphically in figures 1 to 3. In each figure are plotted all the stations at which plankton hauls were made, with the stations of a cruise joined by a continuous line. Short lines perpendicular to this line represent stations at which hauls were made but no specimens taken. At each station where pteropods occurred, a circle has been plotted with diameter proportional to the logarithm of the total number of specimens taken by all the hauls made there. Several examples of the numbers represented by different sizes of circles are given in the legends of the figures. Swarms which were noted in the plankton records are shown by the largest circles.

While one of each of the three kinds of hauls was made at most of the stations, in a few cases only one or two hauls were made. For this reason the quantities of the same species occurring at different stations are not strictly comparable, but quantities of the different species taken at any particular station are comparable. In any case only a very general idea of the distribution of a species in a certain region can be obtained from the data of plankton hauls unless a very large number of hauls have been made over a long time. This is partly due to the tendency of plankters to congregate in shoals. Bigelow (1928) points out that this tendency is very characteristic of *L. retroversa* and it would be expected for the other species.

Comparison of the three figures shows that *C. limacina* and *L. helicina* had very similar distributions, differing from *L. retroversa* in several respects.

Consideration of the stations of the Canadian Fisheries Expedition of 1914-

1915 shows that *C. limacina* and *L. helicina* had similar distributions in that they occurred at the spring stations in greater numbers than at the summer stations

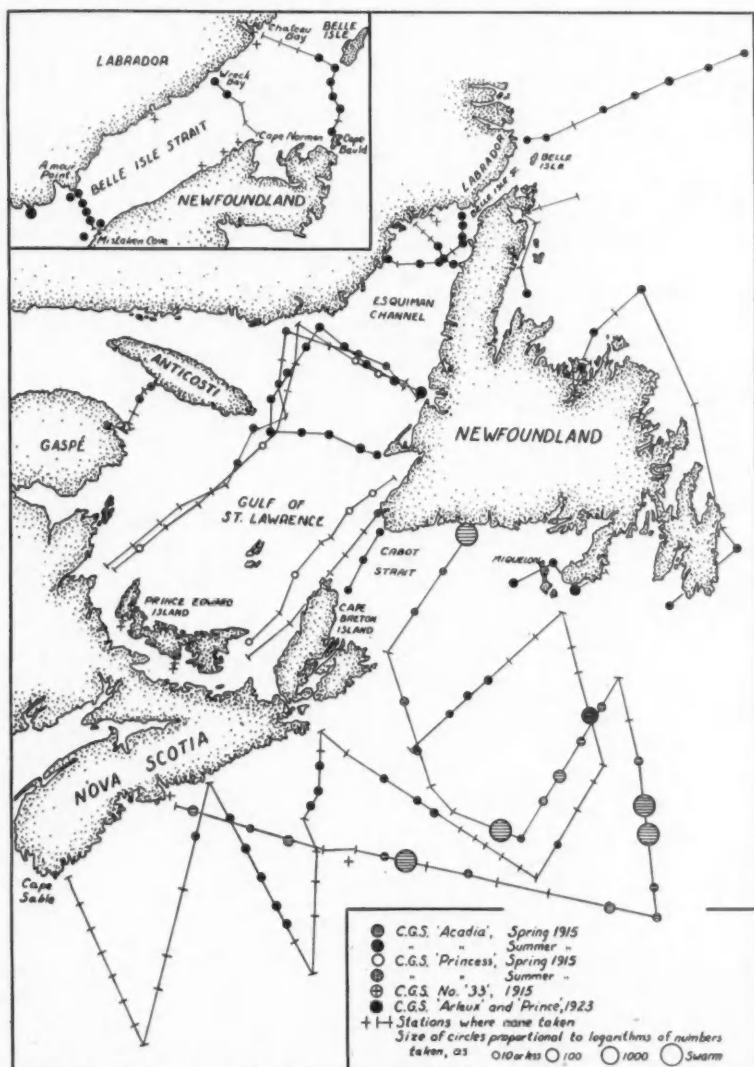


FIGURE 1. Distribution of *Clione limacina* in southern region.

east of Nova Scotia and Cape Breton island. Both species were absent at all the summer stations off the west end of Nova Scotia, but *L. helicina* did not occur at a number of summer stations to the east, where *C. limacina* was taken. Both





small numbers at the "Acadia" stations near the Nova Scotia coast and at some "Princess" stations inside the gulf of St. Lawrence. In summer, *L. retroversa*

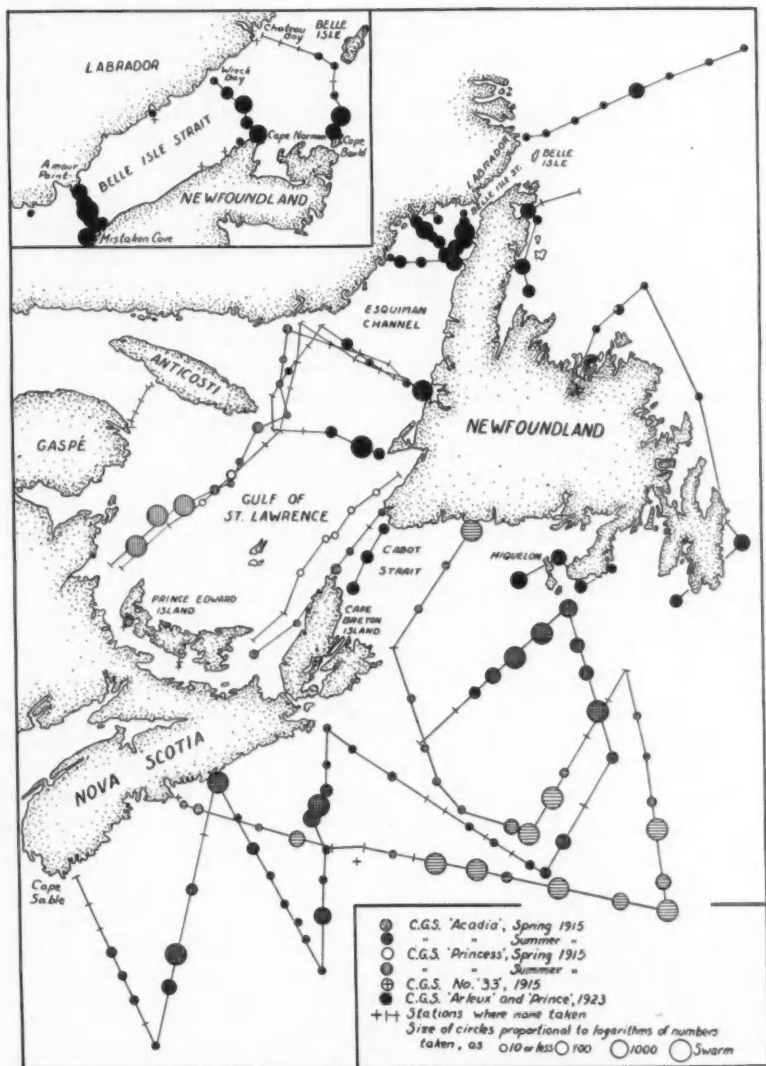


FIGURE 3. Distribution of *Limacina retroversa* in southern region.

occurred at the most southern "Acadia" stations where *C. limacina* and *L. helicina* were absent, and was very abundant south of Miquelon. At the other "Acadia" stations where it had been most abundant in spring, it was now present in small

numbers. Inside the gulf of St. Lawrence, *L. retroversa* was present in summer at southern stations in large numbers where *C. limacina* and *L. helicina* were absent.

Both *C. limacina* and *L. helicina* were taken at some "No. 33" stations between Anticosti and Gaspé while *L. retroversa* was absent from all these stations.

There was little difference in distribution of the three species at the "Arleux" stations. In Belle Isle strait all were well distributed at the western stations between Amour point and Mistaken cove, while at the eastern end between Wreck bay and cape Norman they were all present at the most northern stations. Farther east all the species were absent at the northern stations between Belle isle and Chateau bay, but present at the most southern stations between Belle isle and cape Bauld. At the stations running off the coast of Labrador into the Atlantic ocean, all three species were present at the stations farthest from shore, but *C. limacina* was absent from one and *L. helicina* from three stations near the coast. Around the coast of Newfoundland all species were distributed generally, although *C. limacina* was absent from a number of stations along the east coast. *L. retroversa* occurred at most of the stations and was abundant along the west coast. In Esquiman channel there was a widespread distribution of all species at the "Arleux" stations although *C. limacina* was absent from a number of stations at the east end of the channel along the north shore.

Throughout the southern region *L. retroversa* was considerably more abundant than either of the other species, and *L. helicina* was generally more abundant than *C. limacina*.

#### NORTHERN REGION

The distribution of pteropods in collections from Hudson bay northward is shown in figure 4. Only *C. limacina* and *L. helicina* were taken, and the latter was commonly more abundant. For example, in the shore collections in Hudson strait, 26 specimens of *C. limacina* were taken at 4 stations as compared with 40 specimens of *L. helicina* at 2 stations, and in the plankton tows in Hudson bay, 48 specimens of *C. limacina* were taken at 10 stations while 1,479 specimens of *L. helicina* were taken at 13 stations. Only sample specimens were preserved in the arctic collections, but Mr. Oughton reports that at Craig harbour and Ponds inlet only a few *C. limacina* but many *L. helicina* were observed.

#### DISCUSSION

It is not possible from the available data to reach any definite conclusions regarding correlation of the distribution of the pteropods with conditions of temperature, salinity or light. However, consideration of the ranges of distribution of the three species as given in the literature, and of temperature conditions and current movements of the waters of the region, allows some suggestions to be made to account for several features observed above.

Bigelow (1928) in describing the distribution of plankton in the gulf of Maine considers *C. limacina* and *L. helicina* to be Arctic visitors, whereas *L. retroversa* is a boreal form and a permanent pelagic inhabitant of the gulf, ranging in the western Atlantic from latitude about 34°N. to the southern part of Davis strait.

*L. helicina* is considered to be an indicator of cold currents in the gulf, rarely appearing there, while *C. limacina* occurs more regularly, having seasonal appear-



FIGURE 4. Distribution of pteropods in northern region. Localities in Hudson bay are numbered stations of the S.S. "Loubayne" at which material was obtained by Mr. Hachey. In Hudson strait, Mr. Johansen's collections were at cape Wolstenholme and Wakeham bay; and Mr. Taylor's at Nottingham island, Sugluk inlet, and Port Burwell. At the far north Mr. Rogers' collections were at Fort Ross, Arctic bay, and Lancaster sound; Mr. Shortt's at Thule, Greenland; and Mr. Oughton's at Craig harbour and Ponds inlet.

ance with maximum occurrence from February to May and minimum occurrence in the fall.

Johnson (1934) gives the range of these pteropods as *C. limacina*: Davis

strait to N. 37°; *L. helicina*: Arctic sea to the gulf of Maine; *L. retroversa*: Davis strait to Massachusetts. Thus it appears that all three species can tolerate waters as far north as Davis strait at least, but differ in their toleration of warm waters to the south.

The absence of *C. limacina* and *L. helicina* from the southern "Acadia" stations off Nova Scotia (figs. 1 and 2) may have been due to the high temperature of the water there (Sandström 1919), and the presence of *C. limacina* at a number of summer stations with high temperatures where *L. helicina* was absent, suggests that the former species can tolerate a higher temperature. Similarly the presence of these species at southern "Princess" stations in the spring and their absence in the summer when the water was warmer suggests a temperature effect. It may also be significant that these species were present in much larger quantities at the outer "Acadia" stations south of Newfoundland in spring than in summer when the water there was warm.

The presence of *L. retroversa* at the warm water "Acadia" stations south of Nova Scotia where *C. limacina* and *L. helicina* were absent (fig. 3) probably indicates its ability to tolerate higher temperatures than the latter species. The more widespread distribution and greater abundance of *L. retroversa* at "Princess" stations in summer than in the spring may be the result of the migration of this species into the gulf of St. Lawrence from its centre of abundance farther south as the season progressed. The entrance of water into the gulf of St. Lawrence from the south through Cabot strait and the counterclockwise movement of water within the gulf (Sandström 1919) may account for the abundance of *L. retroversa* along the west coast of Newfoundland in summer.

The distribution of *C. limacina* and *L. helicina* in the northern region (fig. 4) is in agreement with the summary of distribution records for pteropods given by Pelseneer (1887, 1888), with the addition of records for both species in Hudson bay. While no collections are available to furnish information on the northern distribution of *L. retroversa* beyond the stations off Labrador shown in figure 3, its absence at all the stations shown in figure 4 is noteworthy.

Water from the arctic region can enter Hudson bay from Fox basin or by way of Hudson strait where it is carried toward Hudson bay along the north shore in an eastward direction by the rotation of the earth. In Hudson bay the water circulates in a counterclockwise direction and plankton entering the bay with the arctic water is carried in this manner around the bay. As *C. limacina* and *L. helicina* occur in the arctic seas, they would be expected to occur in Hudson bay if they could survive the estuarial character of the water described by Dr. Huntsman (1931), and this has been shown to be the case, as both species occurred throughout the bay.

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Studies of Fish Spoilage  
**VII. Dimethylamine Production in the Spoilage of Cod Muscle  
Press Juice**

BY S. A. BEATTY AND V. K. COLLINS  
*Atlantic Fisheries Experimental Station*

(Received for publication January 3, 1940)

ABSTRACT

Although as yet the precursor is unknown, the mechanism of dimethylamine production in spoiling cod muscle press juice appears to be similar to that of trimethylamine production.

In a previous communication from this laboratory (Beatty 1938), it was concluded that the only volatile bases produced in significant amounts during the spoilage of cod muscle press juice are trimethylamine and ammonia. No method sufficiently sensitive to demonstrate the presence of monomethylamine or dimethylamine was found. Based on indirect methods it was concluded that at least 94 per cent of the volatile bases could be accounted for as either ammonia or trimethylamine.

By the use of a colorimetric method developed by Reay (1937), Shewan (1937) showed that dimethylamine is produced in very small amounts during the spoilage of haddock muscle, previous to the production of trimethylamine.

The present work was undertaken to determine if bacteria are responsible for the production of dimethylamine and, if so, what role the precursor of the amine plays in the metabolism of the micro-organisms concerned.

ANALYTICAL PROCEDURE

The juice used was obtained by taking muscle from codfish before it had gone into rigor, and then mincing and pressing it. All the volatile bases in a 5-ml. sample of the juice were distilled into an excess of acid in the Beatty-Gibbons (1937) modification of the Parnas-Mozolowski still, the excess acid neutralized, and water added to the distillate to make a probably satisfactory concentration of dimethylamine. Suitable aliquots of these neutral solutions were analysed for dimethylamine by means of Dowden's (1938) method in conjunction with the Evelyn photoelectric colorimeter. Trimethylamine was calculated by subtracting the dimethylamine value so obtained from the total volatile bases not bound by formaldehyde (Beatty and Gibbons 1937).

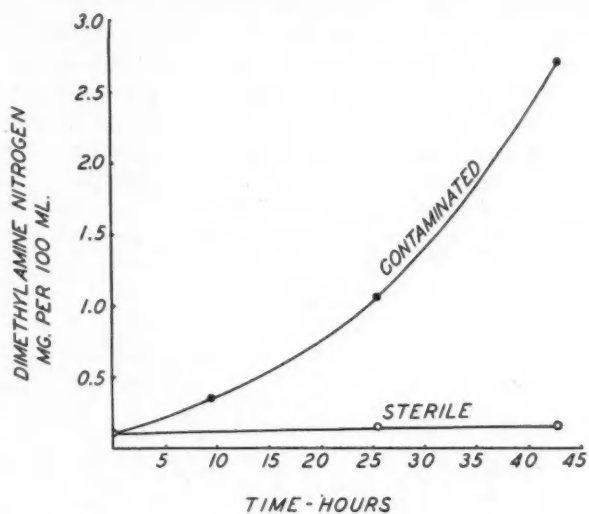


FIGURE 1. The production of dimethylamine in sterile and contaminated cod muscle press juice at 25°C.

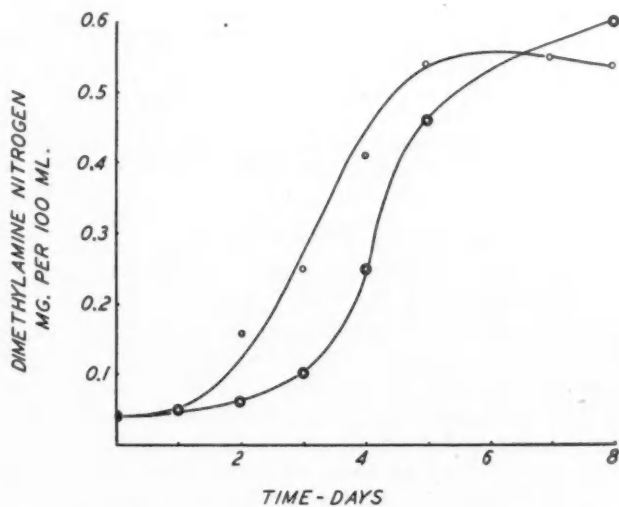


FIGURE 2. The production of dimethylamine by spoilage bacteria in cod muscle press juice stored at 5°C. (Single circles give data for the experiment without air, and double circles for that with air.)

## WHAT PRODUCES DIMETHYLAMINE?

To determine whether dimethylamine is produced by autolytic enzymes or bacteria, its development was followed in juice, part of which was stored as obtained, thus containing the micro-organisms which found their way into it during its preparation, and part of which was sterilized by filtration through a Seitz EK filter. Figure 1 shows the increases in the amounts of dimethylamine in filtered and unfiltered press juice at 25°C. There does appear to be a non-bacterial production of dimethylamine, but it is so small as to be barely measurable. In contrast the bacterial production of dimethylamine is rapid.

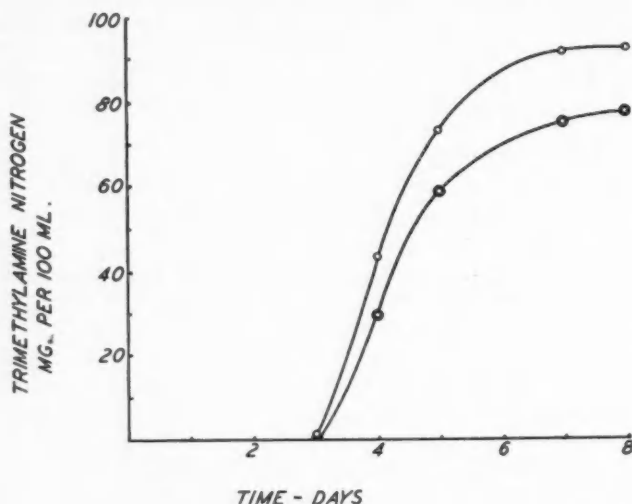


FIGURE 3. The production of trimethylamine by spoilage bacteria in cod muscle press juice at 5°C. (Single circles give data for the experiment without air, and double circles for that with air.)

## THE EFFECT OF AIR

The role of trimethylamine oxide in the respiration of certain bacteria associated with spoilage in sea fish is now known. An attempt was made to determine if the precursor of dimethylamine also acts as a hydrogen acceptor in the oxidation-reduction reactions resulting from the proliferation of these bacteria. Juice prepared without special precautions to avoid contamination was stored in the presence of air and out of air as in previous work (Watson 1939), at 5°C., and analysed at intervals for dimethylamine and trimethylamine. The results for dimethylamine and trimethylamine are shown separately in figures 2 and 3. It will be seen that dimethylamine increases before trimethylamine during the spoilage period, as was found by Shewan, and that this occurs both in the presence and in the absence of air. Figures 2 and 3 show that both dimethylamine and trimethylamine develop more rapidly in the absence of air. This suggests



that dimethylamine as well as trimethylamine has a precursor which acts as a hydrogen acceptor in the oxidation-reduction reactions that occur during the proliferation of certain bacteria.

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## Effectiveness of Ice containing Sodium Nitrite for Fish Preservation

BY H. L. A. TARR AND P. A. SUNDERLAND  
*Pacific Fisheries Experimental Station*

*(Received for publication January 10, 1940)*

### ABSTRACT

Bacterial spoilage of dressed halibut, pink salmon and black cod is markedly inhibited by icing with crushed ice containing small amounts (0.1 or 0.5 per cent) of sodium nitrite instead of ordinary ice, as demonstrated by bacteriological examination and organoleptic tests, including appearance (halibut excepted), odour and taste. Halibut becomes a marked yellow on the ventral (white) surface. Sodium nitrite ice preserves fish much more efficiently than benzoic acid ice.

In a previous communication (Tarr and Bailey 1939) it was shown that ice containing 0.1 per cent of benzoic acid exerted very little beneficial effect on the keeping quality of black cod and halibut, as judged by viable bacterial counts and trimethylamine content of the muscle. Hjorth-Hansen and Karlsen (1939) have since shown that ice containing 0.012 to 0.015 per cent of hydrogen peroxide effects only a slight improvement in the keeping quality of dressed fish and fillets. The fact that nitrites are much more effective than benzoates for preserving both fresh and lightly smoked fillets (Tarr and Sunderland 1939a, 1939b; 1940) suggested the possibility of employing ice containing nitrite to preserve dressed fish. The results of experiments designed to test this point have already been briefly described (Tarr and Sunderland 1939c), and are recorded in detail herewith.

### METHODS

While benzoic acid ice, (Bedford unpub.) can readily be prepared as a true eutectic compound from an aqueous solution containing approximately 0.156 per cent of the chemical, sodium nitrite, when used in similar amounts naturally tends to become concentrated in the liquid phase during the freezing process, preventing uniform distribution. However, experiments have shown that a considerable proportion of the sodium nitrite is scattered mechanically (occluded) throughout the mass, as has been found to be the case with ice made from weak hydrogen peroxide solutions (Hjorth-Hansen and Karlsen 1939). Just as agitation of water during freezing facilitates the concentration of impurities in the centre "core" of the ice blocks, so does aeration concentrate the sodium nitrite, as is evident in table I. It is therefore obvious that in preparing sodium nitrite ice the water containing this salt should not be aerated (stirred) during freezing, and that the cores of the resulting ice blocks should not be "drawn" and refilled

with water as is customary. When blocks of ice containing sodium nitrite are crushed preparatory to use, a fairly uniform distribution of the salt throughout the finely divided particles results (table I).

TABLE I. Distribution of sodium nitrite in 400 lb. (182 kg.) blocks of ice\* prepared from aerated and non-aerated 0.05 per cent (500 parts per million) aqueous solutions of the salt.

Region of block sampled	NaNO <sub>2</sub> in parts per million	
	Aerated during freezing	Not aerated during freezing
Surface sample, not over 2 cm. deep, about 3 cm. from base of block . . . . .	28	408
Surface sample, not over 2 cm. deep, about half way from base . . . . .	12	392
Top corner, not over 5 cm. deep . . . . .	6	500
Core, about 5-7 cm. diameter, 1/3 way from base . . . . .	7500	1480
Core, about 5-7 cm. diameter, 2/3 way from base . . . . .	8000	2420
Core, about 5-7 cm. diameter, at top of block . . . . .	6500	1290
About 3 kg. of melted ice after crushing and mixing thoroughly . . . . .	490	512

\*Frozen in vertical tanks in brine for about 2 days at 10°F.

Samples for determination of the viable bacterial population of the fish muscle were taken from the poke region in the case of halibut, and from one side of the fish in the case of pink salmon and black cod, the technique of making bacterial counts and excising the muscle being identical with that previously described (Tarr and Bailey 1939). Organoleptic tests were made by the writers, and included the external appearance of the iced fish, the odour of the poke, and the taste of the flesh ("belly muscle" in the case of halibut) after cooking for 10 minutes at about 300°C. in an electric oven. The amount of sodium nitrite in treated fish muscle was determined by the method described elsewhere (Tarr and Sunderland 1940).

## EXPERIMENTS

### EXPERIMENT 1.

Twelve halibut (*Hippoglossus stenolepis*), weighing from about 5 to 20 lb. (2 to 9 kg.), were dressed and the pokes scraped and washed with sea water in the usual manner on board a fishing boat soon after capture. Six fish were iced with ice containing 0.5 per cent sodium nitrite and six with tapwater ice. They were landed after 2 days, re-iced with their respective ices, and were stored in boxes in the ice room of a local fish company, fresh ice being added at intervals to replace that which had melted. Individual fish were removed from time to time in order to determine the extent of spoilage. The results are recorded in table II.

### EXPERIMENT 2.

Ten halibut weighing from about 8 to 10 lb. (3.5 to 4.5 kg.) were obtained from a local fish company. These fish had been dressed, washed and iced on

TABLE II. The influence of ice containing 0.5 per cent sodium nitrite on the keeping quality of halibut.

Age of fish in days after capture	Count of viable bacteria in poke muscle (colonies per g.)		Results of organoleptic tests*		NaNO <sub>2</sub> in p.p.m. of wet muscle in fish stored in ice containing nitrite	
	Tapwater ice	Ice containing NaNO <sub>2</sub>	Fish from tapwater ice	Fish from ice containing nitrite	Poke muscle**	Belly muscle**
8	2,400	80	No noticeable difference in odour of pokes nor in flavour of cooked flesh		....	....
12	142,000	8,420	Odour of poke: "Sour"	"Fresh"	880	323
16	980,000	480	Odour of poke: Very sour	Not unpleasant, apparently fresh.	855	500
			No difference in flavour observed on cooking			
19	1,560,000	113	Putrid odour, fish covered with brownish - yellow slime.	Odour not unpleasant, faint smell resembling nitric oxide.	....	....
			No difference in flavour of cooked fish			
26	13,800,000	2,520	Fish very putrid, surface covered with brownish slime.	Odour not unpleasant, faint smell resembling nitric oxide.	....	....
			Cooked flesh: Stale and inedible	Edible and apparently fresh		
31	10,480,000	46,000	Fish very putrid	Odour not unpleasant, faint smell resembling nitric oxide	970	....
			Cooked flesh: Slightly stale, rather "tasteless".	Edible, but dry and rather tasteless		

\*Halibut stored in nitrite ice invariably develop a yellow discolouration. A piece of muscle about midway along the white (ventral) side opposite the poke was used in tasting.

\*\*These terms were described in a previous paper (Tarr and Bailey 1939).

board a fishing boat and were landed 5 to 6 days after catching. Five fish were re-iced with ice containing 0.1 per cent sodium nitrite and five with tapwater ice. They were stored and re-iced as in Experiment 1, individual fish being examined at intervals (table III).

### EXPERIMENT 3.

Pink salmon (*Oncorhynchus gorbusha*) weighing 4 to 5 lb. (about 2 kg.) which had been stored, without being gutted, for about 2 days in ice after capture, were

TABLE III. The influence of ice containing 0.1 per cent sodium nitrite on the keeping quality of halibut.

No. of days fish stored in the experimental ices	Count of viable bacteria in muscle (colonies per g.)		Results of organoleptic tests*		NaNO <sub>2</sub> in p.p.m. of wet muscle in fish stored in ice containing nitrite	
	Tapwater ice	Ice containing NaNO <sub>2</sub>	Fish from tapwater ice	Fish from ice containing nitrite	Poke muscle	Belly muscle
9	1,320,000	288	External appearance: Good Odour of poke: Sour No difference in flavour observed on cooking	Good Fresh	350	....
13	6,800,000	24,800	External appearance: Fair Odour of poke: Very sour No difference in flavour observed on cooking	Good Fresh	370	....
17	15,800,000	122,000	Odour of poke: Very putrid No difference in flavour observed on cooking	Not unpleasant	258	65
20	6,380,000	474,000	External appearance: Poor, fish covered with brownish-yellow slime Odour of poke: Very putrid Cooked flesh: Stale and inedible	Good Not unpleasant Good condition, edible	262	74
22	520,000	118,000	Appearance and odour of the two fish examined about the same as after 20 days Cooked flesh: Edible, good condition	Edible, good condition	134	....

\*See footnote, Table II.

used. Five fish were iced with ice containing 0.1 per cent of sodium nitrite and five with tapwater ice. They were stored, re-iced and examined as in the previous experiments, with the results recorded in table IV.

#### EXPERIMENT 4.

Ten black cod (*Anoplopoma fimbria*) weighing from about 4 to 5 lb. (2 kg.) were selected from a load of fish which had been 5 to 7 days in ice after dressing on board a fishing boat. Half the fish were iced with ice containing 0.1 per cent of sodium nitrite, and the remainder with tapwater ice. They were stored in a room having a temperature of 1.5 to 4°C., and were examined as in previous experiments (table V).

TABLE IV. The influence of ice containing 0.1 per cent of sodium nitrite on the keeping quality of pink salmon.

No. of days fish stored in the experimental ices	Count of viable bacteria in muscle (colonies per g.)		Results of organoleptic tests		NaNO <sub>2</sub> in p.p.m. of wet muscle in fish stored in ice containing nitrite. Muscle from one side of fish sampled as in making bacterial counts
	Tapwater ice	Ice containing NaNO <sub>2</sub>	Fish from tapwater ice	Fish from ice containing nitrite	
9	7,200	264	No difference in odour, external appearance or flavour observed.		267
13	178,000	12,800	No noticeable difference in external appearance. Odour of poke: Sour      Fresh Cooked flesh:              Slightly stale      Fresh		89
17	1,180,000	154,000	External appearance:      Very slimy, stale      Good Odour of poke:              Very stale      Fresh Cooked flesh:              Stale, almost inedible      Edible, good condition		
20	740,000	780	External appearance:      Covered with brownish-yellow slime      Good Odour of poke:              Putrid      No unpleasant odour Cooked flesh:              Stale and inedible      Edible but tasteless		302
22	3,444,000	8,400	External appearance:      Covered with brownish-yellow slime      Fair Odour of poke:              Very putrid      No unpleasant odour Cooked flesh:              Stale and inedible      Edible but tasteless		148

## DISCUSSION

That ice containing 0.1 per cent of sodium nitrite is much more effective in inhibiting the growth of bacteria on dressed fish than is ice containing an identical proportion of benzoic acid is evident when the results of experiments described in this paper are compared with those previously recorded (Tarr and Bailey 1939). Nitrite-containing ice also has the advantage that it preserves both

TABLE V. The influence of ice containing 0.1 per cent of sodium nitrite on the keeping quality of black cod.

No. of days fish stored in the experimental ices	Count of viable bacteria in poke muscle (colonies per g.)		Results of organoleptic tests		NaNO <sub>2</sub> in p.p.m. of wet muscle in fish stored in ice containing nitrite. Muscle from one side of the fish sampled as in making bacterial counts
	Tapwater ice	Ice containing NaNO <sub>2</sub>	Fish from tapwater ice	Fish from ice containing nitrite	
5	300	20	No noticeable difference in external appearance Odour of poke: Sour    Fresh		88
11	3,260,000	1,120	External appearance: Covered with brownish - yellow slime Odour of poke: Very sour Cooked flesh: Slightly stale		67
			Good Fresh Edible, apparently fresh		
13	552,000	51,400	External appearance: Covered with brownish - yellow slime Odour of poke: Very putrid Cooked flesh: Slightly stale, flat		350
			Good Slightly sour Edible, apparently fresh		
14	860,000	31,600	Fish in about the same condition in all respects as after 13 days in the experimental ices.		74
16	1,960,000	45,800	External appearance: Similar to that after 13 days Odour of poke: Very putrid Cooked flesh: Stale and practically inedible		...
			Fair Slightly sour Edible, not unpleasant		

recently caught fish and fish which have been stored for some days in ordinary ice. This is probably partly due to the fact that sodium nitrite readily penetrates the fish muscle, and that it is undoubtedly a much more effective preservative for fresh and smoked fish than is benzoic acid when used in similar (per cent) concentration in brines in which fillets are immersed (Tarr and Sunderland 1939a, 1939b, 1940). Ice containing 0.5 per cent of sodium nitrite causes treated fish

So far, no attempt has been made to overcome the yellow discolouration which arises when the white ventral surface of halibut comes in contact with nitrite-containing ice. No such obvious discolouration has been noticed in either pink salmon or black cod which have been stored in nitrite-containing ice, though freshly clotted blood in the poke region becomes brown due, probably, to the formation of methaemoglobin (Brooks 1937). Mention should be made of the fact that nitrite may in certain instances cause the formation of a very faint pink colour in the muscle of white fish, and increase the intensity of the red colour of the flesh of salmon. The probable cause of this has been referred to elsewhere (Tarr and Sunderland 1939b, and unpub. M.S.). It is intended to pursue this investigation further in the near future.

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## Relation of "Catch per Unit Effort" to Abundance and Rate of Exploitation\*

BY W. E. RICKER

*Indiana University, Bloomington, Indiana*

*(Received for publication January 10, 1940)*

### ABSTRACT

Two extreme types of fisheries are set up for analysis. In type I natural mortality and recruitment are negligible while fishing is in progress; in type II natural mortality, recruitment and fishing mortality all occur throughout the year at a uniform rate. With either type, the catch per unit effort is proportional to the average population on hand *while fishing is in progress*. This statistic is less useful than it may appear, because, in cases of type I, recruitment occurs between the fishing seasons, and in cases of type II, the slow process of removal (or replacement) of accumulated stock following a change in fishing effort makes it difficult to determine the significance of any change in catch per unit effort.

A more useful statistic is the rate of exploitation (a fish's annual expectation of death by capture). A theoretical relationship between rate of exploitation and gear in use is here developed for type I fisheries, and is shown to apply fairly well to many cases of type II—so that if rate of exploitation for one year be determined, that for other years can be calculated. For certain special cases of type I fisheries, several methods are proposed by which rate of exploitation might be estimated from ordinary statistics of catch and effort. For other cases of type I, and all cases of type II, an application of Petersen's tagging technique, or data from other outside sources, appear almost essential to determination of the rate of exploitation.

### INTRODUCTION

Wherever there exists commercial exploitation of an animal species, from which catch records can be obtained, there is a possibility that such records can be used to estimate changes in the abundance of the animal in question. The importance and usefulness of a knowledge of animal numbers, both in theoretical and practical biology, does not need amplification. An attempt therefore to elucidate some of the theoretical aspects of the difficult task of translating catch records into terms of population abundance will be of interest both to ecologists and to those bearing administrative responsibility. What follows is written largely with *fish* populations in mind, but the principles used may be extended to other groups of animals.

The abundance of that part of an animal population old enough or large enough to be of direct interest to man is affected by three factors: human exploitation, "natural" mortality (all that is not caused directly by man), and the

\*Joint contribution from the Pacific Biological Station, Fisheries Research Board of Canada, Nanaimo, British Columbia; and from the Department of Zoology, Indiana University, Bloomington, Indiana (contribution no. 281).

recruitment of its numbers from younger stock. A distinction must be drawn at the very beginning of the discussion, regarding the time at which man's toll is taken.

Type I. Human exploitation takes place at some time of year when recruitment is not operative, and natural mortality nil or negligible; or alternatively, when recruitment and natural mortality are approximately in balance. A possible example of this situation would be a population of game birds, subject to a relatively short hunting season at a time when all individuals are full grown, and subject to a natural mortality which, during that season, is negligible compared to the hunting toll. Among fishes, a fairly close approximation might be found in a fishery of short seasonal duration, provided this season does not coincide with a time of unusual natural mortality, or recruitment.

Type II. Human exploitation takes place simultaneously with the processes of natural mortality and recruitment. Innumerable variants of this situation are possible, as mortality and recruitment can vary seasonally, each in its own fashion. The particular situation which appears to be the logical antithesis of type I, has the processes of natural mortality, recruitment and exploitation all persisting for the same length of time each year, and at a uniform rate. Any reasonable approximation to this condition may be considered as belonging to type II.

Fisheries of long seasonal duration are not likely to approach, even approximately, the conditions of type I, but may well in some instances be referable to type II. A great many, however, will be of some intermediate type.

#### FISHERIES OF TYPE I

Consider a fishery which attacks the commercially useful portion of a fish population with equal intensity in every part of that population's geographical range, so that fish in any particular locality are just as likely to be caught as those in any other. The same amount of gear is used by the fishery throughout the fishing season, and it remains equally effective throughout that season; i.e., it catches a fixed proportion, per unit of time, of the fish available at that time. Further, the natural mortality among the population during the fishing season must be assumed to be exactly balanced by natural increase during the same time; or at the most, the net excess of one over the other must be negligible in comparison with the fishing mortality. As regards the fishing gear, it must be postulated that it is set so as to cover the range of the population evenly, yet at any given instant the space between separate units (e.g., nets) is sufficient to accommodate any possible increase in the number of units in use. Thus, whatever the amount of gear in use, there can be no competition between units for the fish to be caught *during one and the same instant*.

- Let:
- $p$  be the population at the start of the fishing season;
  - $c$  be the catch up to any time  $t$  in the season. ( $p-c$  is the population remaining at time  $t$ );
  - $m$  be the fraction of the original population which has been caught up to time  $t$  ( $m=c/p$ ); for this fraction the term "fishing mortality" will be reserved;

$c_1$  be the catch up to the end of the fishing season ( $t=1$ );  
 $m_1$  be the fishing mortality up to the season's end ( $m_1=c_1/p$ ); to be called the "fishing mortality rate" or "rate of exploitation".

$r$  be the fraction remaining at time  $t$  ( $r = \frac{p-c}{p} = 1-m$ ).

$r_1$  be the fraction remaining at the end of the season.

$f$  be the fishing effort, i.e., the number of units of gear in use.

From the assumptions above, two conclusions follow. The first is that the population of fish will decrease throughout the fishing season at a rate which at any time is proportional to the number of survivors at that time. In the notation given, this is represented by the differential equation

$$\frac{d(p-c)}{dt} = -k(p-c) \quad (1)$$

where  $k$  is the factor of proportionality. If the initial population be represented by unity, this becomes

$$\frac{dr}{dt} = -kr \quad (2)$$

From this an integrated expression for  $r$  can be had, as follows:

Inverting,

$$\frac{dt}{dr} = \frac{-1}{kr} \quad (3)$$

Integrating,

$$t = \frac{-\log_e r}{k} + C \quad (4)$$

where  $C$  is the constant of integration. But if  $t=0$ ,  $r=1$ , and  $\log_e r=0$ ; hence  $C=0$ .

Transposing,  $-kt = \log_e r$  (5)

Taking antilogarithms,  $r = e^{-kt}$ . (6)

Since the duration of the fishing season is considered a unit of time, then when  $t=1$ ,  $r=r_1=e^{-k}$ ; whence

$$k = -\log_e r_1. \quad (7)$$

The above calculations illustrate some mathematical aspects of an ideal fishery whose effect upon the attacked population is to decrease its numbers during each season according to the exponential law of decrease.

#### EFFECTS OF DIFFERENT AMOUNTS OF FISHING

The second conclusion to be drawn from the assumptions made at the beginning of the last section is: when any very short interval of the fishing season is under consideration, any finite change in amount of gear in use during that interval would be followed by a directly proportional change in the catch made during that interval. It does not follow, however, that what is true of a short interval is necessarily true of a whole fishing season. On the contrary, owing to the greater rate of decrease of the population when a larger amount of gear is in use, that larger amount will soon be acting upon a smaller population than would a smaller amount. Hence the larger amount of gear will catch relatively fewer fish than would the smaller, in the course of the season.

As an illustration, consider a fishery which attacks a population of 10,000 fish in each of two seasons. During the first season 100 units of gear are in use, and they catch 5 per cent per week of the fish available at the beginning of that week, the length of the season being 10 weeks. During the first week the catch will be 500 fish, leaving 9,500 at the beginning of the second; during the second the catch is 475, leaving 9,025 at the beginning of the third; and so on. The values for the whole season are given in table I.

TABLE I. Catch and population remaining in two fisheries, by intervals of tenths.

Time in weeks	Fishing mortality 5% per week			Fishing mortality 10% per week			Ratio of cumulative catches
	Population remaining	Catch	Cumulative catch	Population remaining	Catch	Cumulative catch	
0	10000			10000			
1	9500	500	500	9000	1000	1000	2.00
2	9025	475	975	8100	900	1900	1.95
3	8574	451	1426	7290	810	2710	1.90
4	8145	429	1855	6561	729	3439	1.85
5	7738	407	2262	5905	656	4095	1.81
6	7351	387	2649	5315	590	4685	1.77
7	6984	367	3016	4783	532	5217	1.73
8	6635	349	3365	4305	478	5695	1.69
9	6303	332	3697	3875	430	6125	1.66
10	5988	315	4012	3487	388	6513	1.62

In the second season 200 units of gear are used. Although a week (one-tenth of the fishing season) cannot strictly be considered a "short interval" in the sense used above, the fish caught each week will now be *nearly* equal to 10 per cent of the population available at the beginning of that week, or double what it was before. The catch and remaining population each week are given in table I, and the two population trends are plotted together in figure 1. From the figure it is evident that the weekly catch falls off less rapidly in the first case than in the second. This is confirmed by the figures in the last column of table I, where it is seen that the ratio of the catches in the two seasons, which was 2.0 at the start, has fallen to 1.62 at the end.

It follows, therefore, that the catch for the two seasons was not proportional to the product of (gear in use)  $\times$  (original population); or, in other words, catch per unit of gear would not accurately compare the initial abundance of fish in the two seasons. The comparison is as follows:

Initial population	Gear in use	Catch per unit of gear
10,000	100 units	$4012/100 = 40.1$
10,000	200 units	$6513/200 = 32.6$

Evidently catch per unit of gear does not in this instance provide an accurate measure of the initial abundance of fish in different seasons. What then does the

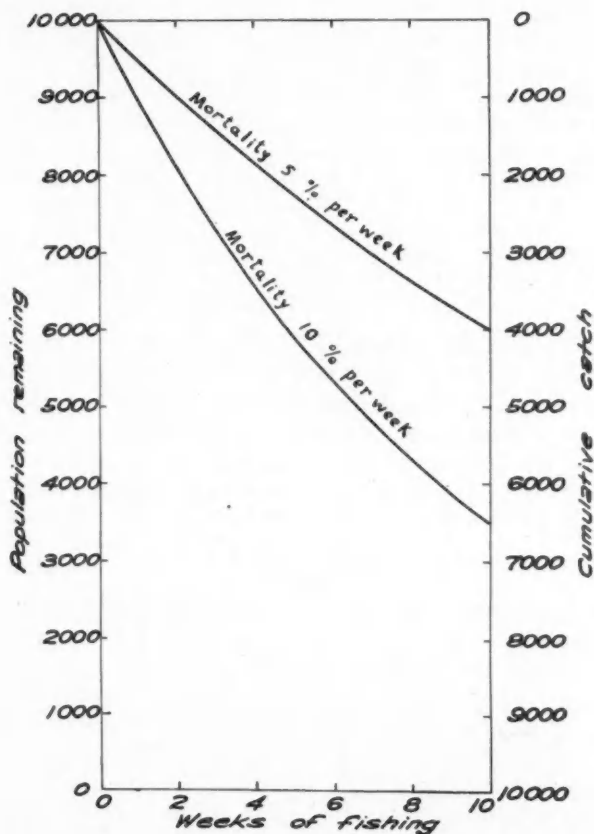


FIGURE 1. Decline in abundance of a fish population exposed to a type I fishery, with two different mortality rates.

ratio of catch to gear measure? Since catch and fishing effort are proportional at successive short intervals of time, it must be that the catch of a whole season is proportional to the product of (fishing effort)  $\times$  (average abundance of fish) during the season. The average populations in the two seasons above can be found, approximately, from table I, by averaging the eleven figures (giving initial

and final abundance half the weight of the others). The averages are 7,825 fish when 100 units were used, and 6,187 when 200 were used. The ratio of the two is  $7,825/6,187 = 1.26$ ; while the ratio of the catch per unit of gear ratios given above is  $40.1/32.6 = 1.23$ . (The small divergence between the two can be ascribed to the approximate method by which average population was determined.)

#### RELATION BETWEEN EXPLOITATION AND GEAR

It would seem, therefore, that it is to an exact measurement of average population in terms of initial population and fishing mortality rate that we should look for information as to the mathematical relation between initial population, catch, and gear in use. Using the same symbols as formerly, and the relationships (1) to (7) above, the average population available for attack in a fishing season of unit length will be represented by:

$$\begin{aligned} \int_{t=0}^{t=1} (p-c) dt &= \int_0^1 p r dt = p \int_0^1 e^{-kt} dt = p \left[ \frac{-1}{k} e^{-kt} \right]_0^1 \\ &= p \left\{ \left( \frac{-1}{k} \cdot e^{-k} \right) - \left( \frac{-1}{k} \right) \right\} = \frac{p(1-e^{-k})}{k} = \frac{-p(1-r_1)}{\log_e r_1} \\ &= \frac{pr_1 - p}{\log_e r_1} = \frac{(p-c_1) - p}{\log_e r_1} = \frac{-c_1}{\log_e r_1} = \frac{-c_1}{\log_e(1-m_1)} = \frac{-c_1}{\log_e(1-c_1/p)} \quad (8) \end{aligned}$$

Or, in words, the average population present during a fishing season is equal to the total catch, divided by the negative natural logarithm of the complement of the rate of exploitation.

As decided above, catch will vary directly as the product of the (fishing effort)  $\times$  (average abundance); or, if  $k$  is the factor of proportionality,

$$c_1 = kf \frac{-c_1}{\log_e(1-m_1)} \quad (9)$$

From this is finally derived an expression relating fishing effort directly with rate of exploitation:

$$\log_e(1-m_1) = -kf \quad (10)$$

The importance of this result will justify including here an alternative and mathematically simpler demonstration, communicated to the writer by Dr. F. A. Davidson. It makes use of the same symbols as defined above, and the same two postulates: that the population fished will decrease throughout a fishing season at a rate which at any given instant of time is proportional (1) to the number of survivors at that time, and (2) to the amount of effort, or gear in use.

If  $k$  is the factor of proportionality, the above postulates can be stated in the following mathematical form:

$$\frac{d(p-c)}{dt} = -kf(p-c) \quad (11)$$

But since  $p$  is a constant,  $dp/dt = 0$ , and therefore

$$\frac{dc}{dt} = kf(p-c) \quad (12)$$

But by definition,  $m = c/p$ , or  $c = mp$ ; hence  $\frac{dc}{dt} = p \frac{dm}{dt}$ .

Substituting these values for  $c$  and for  $dc/dt$  in (12),

$$p \frac{dm}{dt} = kf(p - mp) = kfp(1 - m). \quad (13)$$

Dividing through by  $p$  (since  $p$  cannot = 0);

$$\frac{dm}{dt} = kf(1 - m) \quad (14)$$

Separating variables, and integrating over the area  $t=0$  to  $t=1$ , and hence  $m=0$  to  $m=m_1$ :

$$\int_0^{m_1} \frac{dm}{1-m} = \int_0^1 kft \, dt \quad (15)$$

$$\text{or} \quad \left[ -\log_e(1-m) \right]_0^{m_1} = \left[ kft \right]_0^1 \quad (16)$$

$$\text{or} \quad -\log_e(1-m_1) = kf \quad \text{Q.E.D.} \quad (17)$$

Consider now two different years of a fishery such as the above, with fishing effort and rate of exploitation (fishing mortality rate) represented by  $f_1$  and  $m_1$  in the first year, and by  $f_2$  and  $m_2$  in the second. Following (10) and (17), we may write:

$$-kf_1 = \log_e(1-m_1); \quad -kf_2 = \log_e(1-m_2) \quad (18)$$

Dividing one of these expressions by the other, to eliminate the constant,

$$\frac{f_2}{f_1} = \frac{\log_e(1-m_2)}{\log_e(1-m_1)} = \frac{\log_{10}(1-m_2)}{\log_{10}(1-m_1)} \quad (19)$$

In words, *the logarithm of the complement of the rate of exploitation varies directly as the fishing effort*. Equation (19) is illustrated in figure 2A and B, in which the solid curves show the value of  $m_2$  as  $f_2/f_1$  increases, for various values of  $m_1$ .

The above result is of fundamental importance. At the same time, it will not often be readily applied, even to fisheries which conform closely to the "ideal" type outlined, because the necessary statistical data will not ordinarily be available. In practice, effort ( $f_2$  and  $f_1$ ) may be known for successive years with some accuracy, also catches ( $c_2$  and  $c_1$ ). The latter are related to fishing mortality by the simple expressions:

$$m_1 = c_1/p_1; \quad m_2 = c_2/p_2. \quad (20)$$

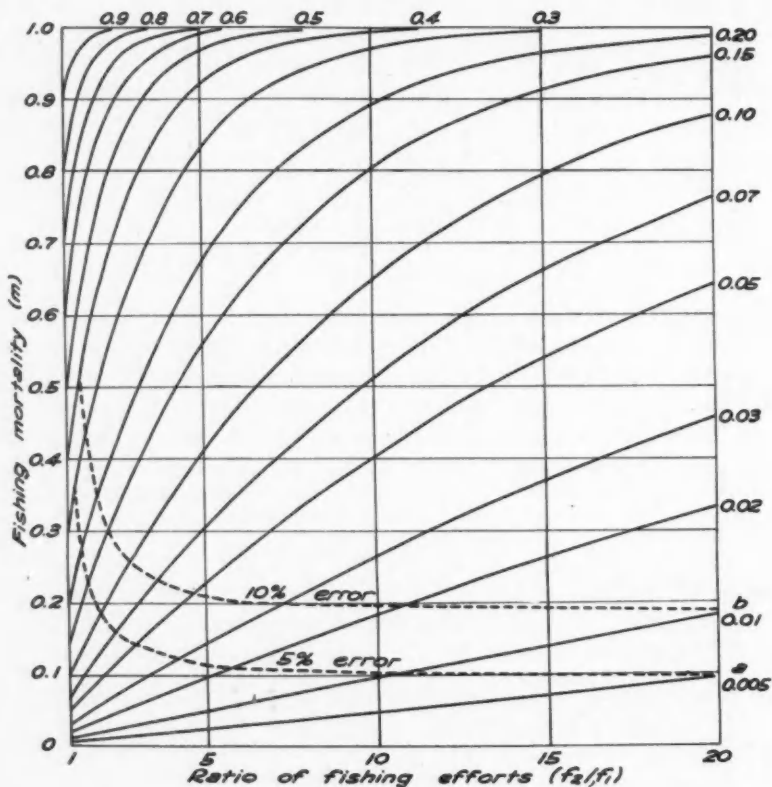
But unless either  $p_1$  or  $p_2$  is known in absolute terms, as is rarely the case, neither value of  $m$  can be determined. *As a general rule, therefore, when the quantity of gear in use varies between successive years of fishing, it will be impossible to use catch per unit effort as an accurate measure of the change in relative abundance of a species at the beginning of each year, unless the absolute value of this abundance be known for one or other of the years.*

## APPROXIMATIONS TO THE FUNDAMENTAL EQUATION

Fortunately there are special cases which permit of an easier computation:

(a) From equations (19) and (20), if  $f_2 = f_1$ , then  $m_2 = m_1$ , and  $c_2/c_1 = p_2/p_1$ . In words, when the total amount of gear in use does not change from year to year, the total catch in each of two successive years is directly proportional to the abundance of fish at the beginning of those years.

(b) In equation (19), as  $m_1$  and  $m_2$  decrease in size,  $(1-m_1)$  and  $(1-m_2)$  approach unity. If both  $m_1$  and  $m_2$  be small, the logarithmic relationship may



A

FIGURE 2. Relation between fishing effort

be approximately represented by a simple proportion, thus:

$$\frac{f_2}{f_1} = \frac{\log(1-m_2)}{\log(1-m_1)} \rightarrow \frac{m_2}{m_1} \quad (\text{when } m_2 \text{ and } m_1 \text{ are small}) \quad (21)$$

In words, when both the first-year and second-year fishing mortality rates are small, rate of exploitation is approximately proportional to fishing effort. Expressed otherwise, when rate of exploitation is low, average population during a year will not differ greatly from initial population, and the catch per unit of gear,

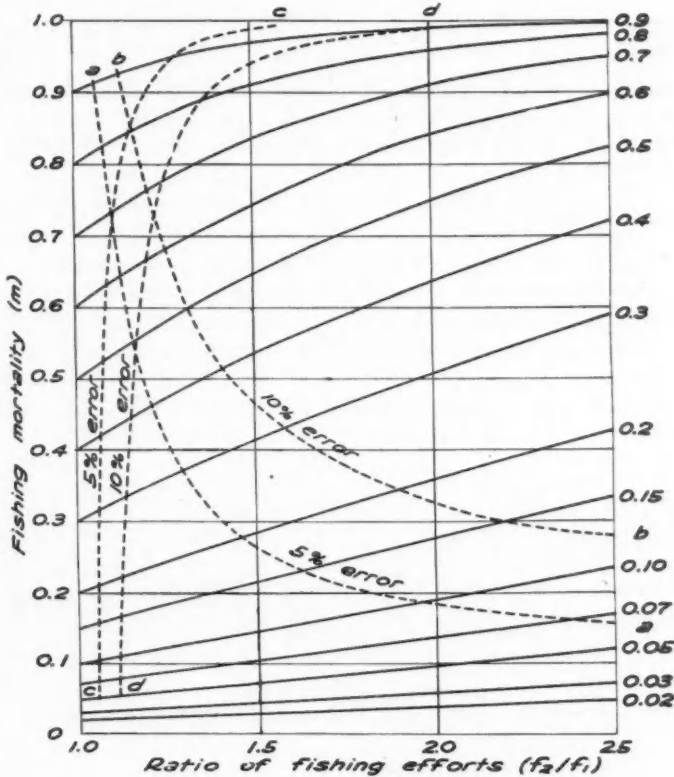


which is proportional to average population, will be also approximately proportional to initial population.

Further, in equation (19), if  $f_2/f_1$  be close to unity the logarithmic relationship may again be transformed into the simple one:

$$\frac{f_2}{f_1} = \frac{\log(1-m_2)}{\log(1-m_1)} \rightarrow \frac{m_2}{m_1} \text{ (as } f_2 \rightarrow f_1 \text{)} \quad (22)$$

In words, when fishing effort does not change much between two years, change



B

and annual fishing mortality (rate of exploitation).

in rate of exploitation will be approximately proportional to change in effort.

As with all approximations, it is necessary to know the limits beyond which equations (21) and (22) become too inaccurate to be useful. In figure 2A and B the limits of their applicability are shown by lines  $a$  and  $b$  for possible errors of 5 and 10 per cent. Any combination of values of  $m_2$  and  $f_2/f_1$  which lies below or to the left of one of these lines can be treated by the approximate method of

equations (21) and (22) without introducing a percentage error greater than that indicated. The position of these lines was determined as follows:

If  $f_2/f_1 = m_2/m_1$  approximately, then  $m_2 = f_2 m_1 / f_1$  approximately. The approximate value of  $m_2$  so calculated will always exceed the true value, if  $f_2 > f_1$ . The difference between the approximate and the true value, divided by the latter, can be equated to any desired degrees of error, in this case the two following:

$$\frac{\frac{f_2 m_1}{f_1} - m_2}{m_2} = 0.05; \quad \frac{\frac{f_2 m_1}{f_1} - m_2}{m_2} = 0.10 \quad (23)$$

From (23) and (19) the positions of various points on lines *a* and *b* were calculated by an approximate interpolative method, carried to the necessary degree of accuracy.

Whenever equations (21) or (22) are appropriate, there follow from (20) the further relationships:

$$\frac{p_2}{p_1} = \frac{c_2 m_1}{m_2 c_1} = \frac{c_2 f_1}{c_1 f_2} = \frac{c_2}{f_2} \div \frac{c_1}{f_1} \quad (24)$$

In these cases, therefore, the *catch per unit of gear* in each of two seasons is directly proportional to the abundance of fish at the beginning of that season.

(c) When the rate of exploitation in one year is quite high (say above 0.9 or 0.95) no amount of increase in fishing effort can produce any very great increase in that rate, which, of course, cannot exceed 1.0. In this situation, if first-year and second-year mortality rates be considered approximately equal, from equation (20),

$$p_2/p_1 \rightarrow c_2/c_1 \text{ (if } m_2 \rightarrow m_1 \text{)} \quad (25)$$

With these high mortality rates catch alone will be approximately proportional to population; and the same approximation can be used at low fishing mortality rates, if  $m_2$  is close to  $m_1$  because  $f_2/f_1$  is close to unity. The regions in which this approximation can be used, without the error involved in assuming  $m_2 = m_1$  exceeding 0.05 and 0.10 respectively, can be calculated from the relationships:

$$\frac{\frac{m_2}{m_1} - 1}{\frac{m_2}{m_1}} = 0.05; 0.10. \quad (26)$$

The lines of demarcation so defined are plotted on figure 2B (lines *c*, *d*). Values of rate of exploitation and of effort lying above and to the left of these lines can be treated as though exploitation remained unchanged, without exceeding the indicated error.

It will be noticed that approximations (b) and (c), given in equations (22) and (25), are of an opposite character. If (b) is used to compare  $p_2$  with  $p_1$ , the value of  $p_2$  obtained will be relatively too small; if (c) is used,  $p_2$  will be relatively too great—provided in both cases that  $f_2 > f_1$ . The true value will lie between the two approximations. As shown above, it may lie very close to either the one or the other, or even (when  $f_2$  does not differ much from  $f_1$ ) close to both. Obviously

there exists, for each value of  $f_2/f_1$ , a value of  $m_2$  with which either approximation is as good as the other. The magnitude of this value can be found by equating expressions (23) and (26):

$$\frac{\frac{f_2 m_1}{f_1} - m_2}{m_2} = \frac{\frac{m_2}{m_1} - 1}{\frac{m_2}{m_1}} \quad (27)$$

which reduces to:

$$\frac{2m_2}{m_1} = \frac{f_2}{f_1} + 1 \quad (28)$$

The previous calculations have not been carried through with sufficient accuracy to define exactly the position of the line representing pairs of  $m_2$  and  $f_2/f_1$  values which satisfy this equation, but it lies between  $m_2=0.7$  and  $0.8$  over the effort range from 1 to 20.

(d) In cases where none of the three above approximations apply, it may sometimes be possible to compare initial abundance in two years by one of two other methods. The first of these follows naturally from approximation (b). If the values catch/gear for the whole of two seasons cannot be used to compare initial abundance because fishing mortality is too great, then possibly a satisfactory comparison can be made with half the data of each year, or with some smaller fraction. By reducing progressively the fishing period under consideration, the value catch/gear tends toward an asymptotic limit, at which point the ratio of catch/gear for the two years is the same as the ratio of their initial populations.

Thus in the example of table I, the ratio of the two years' catch/gear for the whole 10 weeks fishing season was  $40.1/32.6=1.23$ ; for the first 5 weeks only it was 1.10; for the first 2 weeks it was 1.03—approaching the ratio of initial populations, which was 1.00.

An evident criticism of this method is that it is wasteful of data. In some cases only a small part may be usable in this way. A method much more economical in this respect has been suggested to the writer by Dr. O. E. Sette, as follows:

(e) The general form of the integral in equation (16) is

$$-\log_e(1-m) = kft \quad (29)$$

from which it appears that as long as the product  $ft$ , or gear in use multiplied by the time it is in use, is kept constant, fishing mortality ( $m$ ) will be a fixed quantity. But  $m=c/p$ , and  $c$  (catch) being known, the relative value of  $p$  (initial population) in two different years can be compared in any cases where  $ft$  is kept constant. This can be done by adjusting the value of  $t$  (the time under consideration) in one of the years, to make the two products equal.

As an example, consider a fishery in which the gear in use is 100 units in year (1), and only 80 in year (2). Considering the whole fishing season as a unit of time in each instance, the product  $ft$  will be 100 in the first year, 80 in the second. To make these equal, it will be necessary to consider the catch data for

only the first 4/5 of the season in year (1), and compare it with the whole catch of year (2). If the two are equal, then the initial population has not changed between the two years; if unequal, the amount of increase or decrease in population is proportional to the difference in the amount of catch.

Although method (e) still fails to make use of the whole of the catch data available, it is much better in this respect than method (d). It has, however, this serious drawback, that rather strict adherence is required to the postulates of (1) unchanging amount of gear in use within each season, and (2) uniform susceptibility of the individual fish to capture, throughout the season. Relatively small departures from these conditions may lead to large errors.

In general, it is likely that neither of methods (d) and (e) will prove satisfactory in many cases, though either or both may give valuable indications of changes which may be taking place.

#### DETERMINING RATE OF EXPLOITATION BY MARKING

It has been shown that catch per unit of gear will, in an ideal situation, measure the change in average abundance of a fish population between two years, but that change in the initial population in successive years cannot be so measured except in a restricted number of cases, whose applicability to the data at hand may be difficult to prove. It may be asked, why then bother with initial population, if its determination is to prove unduly difficult? Will not average population suffice? A little reflection, however, will show the weakness of the latter concept, when populations of type I are under consideration. The amount of fishing gear in use is one factor governing the size of the average population in a given year. For example, imagine a type I fishery in which the gear in use has increased over a period of years, and catch per unit of gear has diminished. Since the decline in catch per unit would occur even if the initial stock on the fishing grounds remained the same from year to year, this information will not in itself be sufficient to decide whether or not the stock is being reduced.

If none of the methods and approximations discussed above are applicable to a particular case, it will be necessary to obtain an estimate of the actual rate of exploitation, or fishing mortality rate, in at least one year. Having this, the rate of exploitation for other years can be calculated from (19), and the absolute value of initial population abundance in each year can be obtained from (20).

Petersen's (1897) experimental method of estimating rate of exploitation has been in use since before the turn of the century. A known number of tagged or marked fish is liberated at random throughout the population being fished, the proportion of recoveries of such being used as an estimate of the rate of exploitation for the whole population. The method has a number of technical difficulties—for example, the loss of tags from the fish, and possible excess mortality among tagged fish; but a discussion would be out of place here. When recoveries of marked fish extend over several years (or seasons), one appropriate method of calculating the rate of exploitation is given by Thompson and Herrington (1930) and Graham (1938), while another which may prove very useful was recently described by Jackson (1939).

## RATE OF EXPLOITATION BY SUCCESSIVE CATCHES METHOD

A rough calculation of initial population, and hence of fishing mortality rate, can sometimes be made from catch data, supplemented by knowledge of the age-classes in the fishery, and their rate of growth. Briefly, if natural mortality can be disregarded, the population at the beginning of a fishing season may be considered approximately equal to that present at the same time the previous year, minus the catch of that year, and plus the number of new recruits in the second year's population. In the notation used, this is

$$p_2 = p_1 - c_1 + z_2 \quad (30)$$

if  $z_2$  represents the newcomers present in the second year. The value of  $z_2/p_2$  can be obtained from growth studies, in some cases at least. If so, following estimation of mortality rate in one year, that for a second year can be calculated from formula (19), and continued trials will give a result which brings  $c_1$  to the observed figure.

This may be illustrated numerically. Between 1935 and 1936 the catch of squawfish (*Ptychocheilus*) in a certain lake increased from 2,170 to 4,580, while fishing effort increased approximately five-fold. If one quarter of the second year's population was new recruits ( $z_2/p_2 = 0.25$ ), possible values of initial and final fishing mortality rates can be read from figure 2 at  $f_2/f_1 = 5$ , and tabulated along with the corresponding populations by substituting in equation (20):

First year		Second year		First year's catch
$m_1$	$p_1$	$m_2$	$p_2$	$p_1 - 0.75p_2$
0.5	4340	0.969	4730	790
0.4	5420	0.922	4970	1690
0.3	7230	0.832	5500	3110
0.2	10850	0.673	6810	5740

Obviously the value of  $m_1$  necessary to make  $p_1 - 0.75p_2$  equal 2,170 lies between 0.3 and 0.4; by graphical interpolation it is found to be 0.36, the corresponding value of  $m_2$  is calculated from figure 2 as 0.89, and  $p_1$  is close to  $2170/0.36 = 6030$ . That is, the first year's fishing took a little over a third of the fish available, and the second year's took nearly nine-tenths of those remaining, on the assumptions made.

Because natural mortality between the fishing seasons has been ignored in this calculation, the calculated  $p_1$  value will be somewhat too low. If any plausible guess as to out-of-season natural mortality can be made, it can be added to catch ( $c_1$ ) for the purpose of entering the last column of the above schedule. In this way the value of  $m_1$  will be reduced, and that of  $p_1$  increased. Thus, in the example, if 500 fish died naturally between the first and second years, the value  $2,170 + 500 = 2,670$  should be entered in the last column of the schedule, giving by interpolation a value of  $m_1 = 0.33$  and of  $p_1 = 2,170/0.33 = 6,550$  fish approximately.

## RATE OF EXPLOITATION FROM RELATIVE INITIAL ABUNDANCE

If in any way the relative abundance of the initial populations in two successive years can be ascertained, it will be possible to calculate the rate of exploi-

ation in the two years with the usual statistics of catch and effort, provided the effort has not remained unchanged.

From the equations (20) we may write

$$\frac{m_2}{m_1} = \frac{c_2 p_1}{c_1 p_2} \quad (31)$$

If  $x$  be the ratio of the two initial populations, so that  $p_2 = x p_1$ , then

$$\frac{m_2}{m_1} = \frac{c_2}{x c_1} \quad (32)$$

Hence if  $x$  be known, in addition to the catches in the two years, the value of  $m_2/m_1$  can be obtained. But for any given value of  $f_2/f_1$ , a specific value of the ratio  $m_2/m_1$  is associated with specific values of  $m_2$  and  $m_1$  individually. This may be illustrated from figure 2B, for  $f_2/f_1 = 2.0$ :

$m_1$	$m_2$	$m_2/m_1$
1.00	1.00	1.0
0.90	0.99	1.1
0.80	0.96	1.2
0.40	0.64	1.6
0.10	0.19	1.9
0.05	0.097	1.95

Evidently the range of values of  $m_2/m_1$  is from 1.0 to 2.0, as  $m_1$  decreases from 1 to 0. More generally, the range is from unity to the value of  $f_2/f_1$  in question. Figure 3 is plotted to show the magnitude of  $m_1$  for various combinations of  $f_2/f_1$  and  $m_2/m_1$ . Its practical value will be to obtain an estimate of  $m_1$  when the two ratios are known.

Example 1. An example of a situation where figure 3 could be used to estimate rate of exploitation is in the table below. The data are hypothetical, but are modelled after statistics of a trolling fishery for spring salmon, described to the writer by Dr. A. L. Tester:

Year	Effort (no. of lines)	Catch (individuals)	Catch/effort (fish per line)
1.....	636	4080	6.42
2.....	465	3430	7.38
3.....	390	3390	8.70
4.....	300	2830	9.43
5.....	342	3000	8.77
6.....	402	3240	8.05
7.....	474	3780	7.98
8.....	501	3370	6.73
9.....	570	4000	7.02
10.....	660	3919	5.03
11.....	579	3780	6.53
12.....	345	3190	9.25

If these values be plotted, there is evident a decrease in catch per unit of gear as the gear in use increases. Comparison of years in which effort was approximately the same (2 and 7, 3 and 6, 5 and 12, 9 and 11) provides no indication of a progressive change in catch/gear values with time, hence the population too cannot have had any noticeable trend toward increase or decrease, although there may have been some variation from year to year. Since population is essentially unchanged, we may put  $x=1$  in equation (32), so that  $m_2/m_1=c_2/c_1$ .

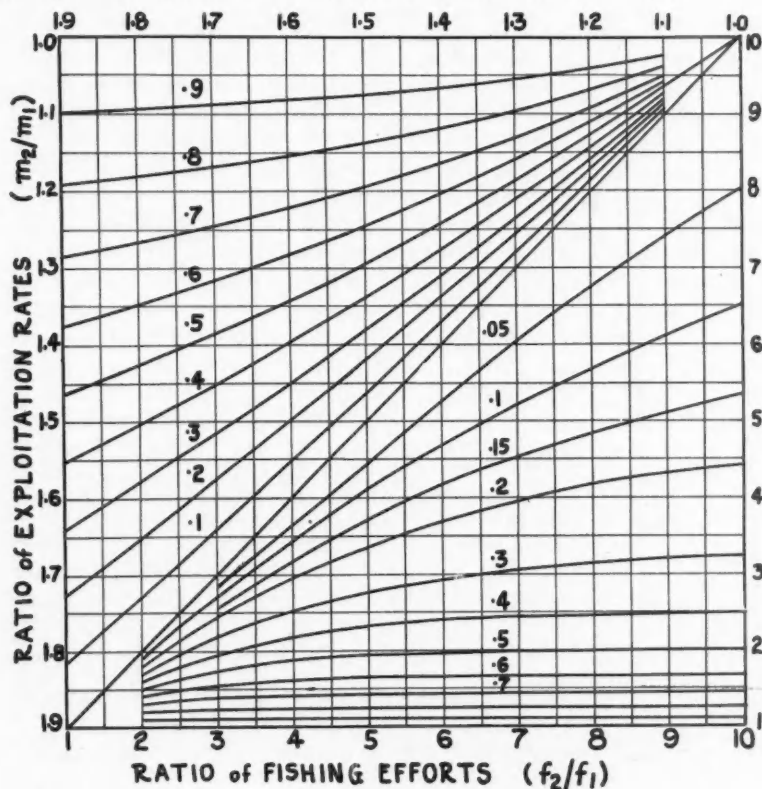


FIGURE 3. Relation between the ratio of fishing efforts ( $f_2/f_1$ ) in two fishing seasons, and the ratio of the exploitation rates ( $m_2/m_1$ ), for various even values of  $m_1$ , which is the rate of exploitation in the season having the lesser fishing effort. Values of  $m_1$  are indicated by the curved lines. The upper left half of the diagram is independent of the lower right, being a large-scale chart of the effort range up to 1.9.

The extreme range of gear used is from 660 to 300 units, whose ratio is 2.20. The corresponding value of  $c_2/c_1$  is 3,910 to 2,830 whose ratio is 1.38. Referring to figure 3, this is found to correspond to an initial mortality rate ( $m_1$ ) of about 0.66. Some improvement in this estimate can be made by drawing the best free-hand line along the graph of catch against gear, and using the catch figures repre-



sented by the points where the line cuts the ordinates representing extremes of gear in use, rather than the actual catch figures. A model showing approximately the amount of curvature to be expected in this line can be drawn as a guide, using 0.66 as the minimum rate of exploitation. In this way an improved estimate of  $c_2/c_1 = m_2/m_1$  is obtained as  $3,950/2,800 = 1.41$ . From figure 3, this corresponds to a mortality rate in year 4 of 0.63, and from equation (19) the others can be calculated. From these and the catch records, population and escapement in each year of the fishery can be calculated as follows:

Year	Rate of exploitation	Population	Escapement
1	0.88	4,600	500
2	0.79	4,300	900
3	0.72	4,700	1,300
4	0.63	4,500	1,700
5	0.68	4,400	1,400
6	0.74	4,400	1,200
7	0.79	4,800	1,000
8	0.81	4,200	800
9	0.85	4,700	700
10	0.89	4,400	500
11	0.85	4,400	600
12	0.68	4,700	1,500

Example 2. A certain fishery attacks a population very uniformly, even over short periods of time. The catch per unit of gear calculated from the first two weeks of fishing, when the fraction of the total population taken is still small, indicates that the available population has increased by one-half between two years ( $p_2 = 1.5p_1$ ;  $x = 1.5$ ). The total catches for the whole fishing period of the two years are in the ratio of 1 to 1.7; the fishing efforts are in the ratio of 1 to 1.3.

From (32), the ratio  $m_2/m_1 = 1.7/1.5 = 1.13$ . Referring to figure 3, with  $f_2/f_1 = 1.3$ , this corresponds to a first-year rate of exploitation of  $m_1 = 0.71$ . The second year's rate of exploitation is therefore, from (32),  $\frac{1.7}{1.5} \times 0.71 = 0.80$ ; or the same result can be read from figure 2B.

#### EXPLOITATION OF MIGRATORY FISHES

Certain fisheries, particularly those attacking anadromous fish, are peculiar in that the fish become vulnerable at some particular point or area along their migration route, and not elsewhere. The migration takes place over a period of time, during which fish are continually entering, and leaving, the fishing area. Such a fishery can be shown to conform to relationship (19) deduced from type I fisheries, given the assumptions of (a) unchanging amount of fishing gear in use within each fishing season, and its uniform efficiency (or a reasonable approximation to these conditions); and (b) a uniform pattern of arrival and departure of the fish, between successive years—i.e., while it is not necessary that the pro-



portion of fish entering the fishery and the average time they remain before leaving should be identical for successive parts of each year, there should be substantial agreement between corresponding parts of successive years in these respects.

#### FISHERIES OF TYPE II

Fisheries of type II differ from those of type I essentially in the fact that the population does not have a chance to recuperate its numbers during a resting-period between one year's exploitation and the next. On the contrary, the loss due to fishing mortality must be made good, if at all, during the time fishing is in progress. The full import of this difference in the present discussion may not at once be obvious. It means, however, that there is no longer the same importance to be attached to the abundance of fish at the *beginning* of a year's fishing. If the fishing is in fact continuous, the rate of change of the population numbers can be traced through a series of years by plotting abundance at *any* given time of year, or by plotting the average abundance for the whole of each year, over the period under consideration. Given a constant fishing effort within each year, this latter will be proportional to catch per unit of gear, as shown under type I fisheries. The catch per unit of gear will in such a case give possibly the most useful information available concerning changes in the population density in the fishery in question.

In spite of this evident simplification, type II fisheries will ordinarily be more difficult to regulate, on the basis of catch returns, than those of type I. The reason is that, in type II, changes in catch and in average population on hand stand in a rather obscure relationship to the amount of fishing effort and consequent rate of exploitation. The nature of this relationship will now be explored, a task that is the easier, because the type of calculation necessary has already been formulated. This was apparently first done by Baranoff (1918), according to Thompson (1937). Neither Baranoff nor Thompson and Bell (1934), however, have dealt with fisheries strictly conforming to type II as here defined, but with a simplified type, in which all recruitment to the fishery is made to take place at a single instant of each year, while natural and fishing mortality persist throughout the year at a uniform rate. This procedure ascribes to the youngest age-class in the fishery, the full mortality rate, and thus to some extent distorts the relationships between mortality and gear in use away from what may be expected in most actual fisheries.

#### MORTALITY AND RECRUITMENT

In place of the single factor, fishing mortality, which alone affected population numbers in type I fisheries during the fishing season, there are in type II three factors to be considered—fishing mortality, natural mortality, and recruitment. In the discussion of fishing mortality in fisheries of type I, it was shown that the number of fish caught during a short period of time would vary directly as the number present, given a constant fishing effort. Natural mortality may also, for want of better information, be imagined to be reasonably well represented by the same mathematical treatment.

It is necessary in this case, however, to distinguish two quantitative aspects of mortality. In what follows *mortality rate* will be used to indicate the annual expectation of death of a fish of catchable size from a given cause, *if no other causes of death were operative*. In the case under consideration, the natural mortality rate ( $n$ ) and the fishing mortality rate ( $m$ ) both contribute to the total mortality rate ( $a$ ). Since the two causes of death compete for the fish available, the total mortality rate must be obtained by adding the first two logarithmically: i.e.,  $\log a = \log n + \log m$ . The element of competition is perhaps better shown by an alternative expression:  $a = m + n - mn$ , in which  $mn$  is the fraction deducted so that no fish will be made to die twice.

The annual expectation of death of a fish from a given cause, *taking other causes of death into account*, will differ from mortality rate as defined above. The annual expectation of natural death ( $\nu$ ), added arithmetically to the annual expectation of death by capture ( $\mu$ ), will give the total expectation of death, which is the same as the total mortality rate: i.e.  $\nu + \mu = a$ . In what follows we shall be most concerned with the expectation of death by capture, and propose to use the familiar term *rate of exploitation* with this exact meaning. The relation of these actual expectations of death to the mortality rates is as follows:

$$\nu = \frac{n}{m+n} (m+n-mn)$$

$$\mu = \frac{m}{m+n} (m+n-mn)$$

The terms "fishing mortality rate" and "rate of exploitation" as defined above are both distinct from the "rate of fishing" of Graham (1938, p. 77), defined as the "catch in a moment of time expressed as a percentage of the stock at that moment"; this, on a per annum basis and for populations in balance, is equivalent to the ratio of the total yearly catch to the stock continuously on hand. "Rate of fishing" may exceed 100 per cent per annum when the number of captures is great, whereas mortality rate and rate of exploitation cannot exceed unity. Though an interesting concept, the rate of fishing is not of much practical utility, because it becomes intangible whenever population numbers are changing, varying widely not only between years, but within a year, even though during that year the fishing effort remain constant. By contrast, any given rate of exploitation can be associated with a definite degree of fishing effort, independent of changes in population density (except when such a change is proceeding very rapidly, as in the second year of table III). Though the relation between the two is not simple, it is not ordinarily variable, as long as the natural mortality rate remains unchanged.

The reader will readily perceive that, with fisheries of type I, "fishing mortality rate" and "rate of exploitation" are the same quantity, and the terms are there used interchangeably. Graham's (1938, p. 82) term "intensity of fishing" is synonymous with our "rate of exploitation", but it has so frequently been used by others in the sense of "fishing effort" that it is not adopted here.

The mathematical treatment of natural increase must be different from that

proposed for mortality. By no stretch of the imagination can recruitment be supposed to proceed at a logarithmic rate—increasing or decreasing as population does throughout a season. Whereas mortality affects all age-classes in the fishery, any increment to the catchable population is of only one or a few age classes—the youngest. The number of such which appear in a given year may be affected by the intensity of fishing a few years previously, but not by that of the current season. For simplicity therefore it has been customary to consider recruitment as uniform from year to year; and in this paper it is also considered uniform within each year.

#### AGE COMPOSITION OF A BALANCED POPULATION

Consider a type II fishery which receives a total of 1,000 recruits each year, these entering at a uniform rate throughout the year. They are, on the average, subject to just one-half of the total mortality which older year-classes in the fishery suffer. If the latter fraction is  $a$ , the newcomers will decrease by  $1000(a/2)$ . The number of their survivors at the end of the first year will therefore be  $1000(1-a/2)$ . Of these, fraction  $a$  are killed the following year, leaving  $1000(1-a/2)(1-a)$  at its end. Similarly the number of survivors a year later is  $1000(1-a/2)(1-a)^2$ , and so on. In a state of balance, where the number of annual recruits and the mortality rates have been fixed for many years, the total stock on hand will be equal to the sum of the above fractions, or

$$1000 \{1-a/2\} \{1+(1-a)+(1-a)^2+(1-a)^3+\dots\} = \frac{1000(1-a/2)}{a}$$

The total mortality in a year will, in a state of balance, be equal to the number of recruits, i.e. 1,000. The fraction that this is of the total population is represented by

$$\frac{1000}{\frac{1000(1-a/2)}{a}} = \frac{a}{1-a/2} \quad (33)$$

The limit of the value of this expression is 2, when  $a=1$ , which gives an upper theoretical limit to the number of deaths annually at 200 per cent of the stock continuously on hand, when population is in balance.

On this plan, an example is presented in tabular form of the number of fish of different ages present at the start of successive years, in columns 2 and 4 of table II. The annual expectation of death of fish already in the fishery  $=a=40$  per cent, that of the newcomers averaging therefore 20 per cent. The total stock on hand at all times is 2,000 fish, and the total deaths are 1,000, equal to the number of recruits.

#### EFFECT OF INCREASED MORTALITY

The even-numbered columns of table II, from 6 onward, show the effect upon the age composition of the population of a sudden increase of the total mortality rate, or expectation of death of fish in the fishery, from  $a=0.4$  to  $a=0.8$ . There is a decrease in stock on hand, rapid at first and more gradual later, until

a new balance is achieved. Concurrently there is a sudden increase, then gradual decline, in the number of fish dying each year, until at the end the equilibrium value of 1,000 deaths per year is restored.

TABLE II. Age classes and mortalities in a hypothetical population. Column 1 assigns numbers to the successive age classes in the fishery, class 1 being the first which is exposed to the full mortality rate. Columns 2 and 4 represent a population composed of 1000 yearly recruits entering at a uniform rate throughout the first year, these being subject to a total mortality rate of 40 per cent per annum in this and subsequent years, from the time they enter the fishery. Even-numbered columns from 6 on show the change in age composition of the population, when the mortality rate is suddenly increased to 80 per cent per annum, up to attainment of a new balance in columns 14 and 16. Odd-numbered columns from 3 onward show the year-class distribution of the total fish dying in successive years.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
0	(1000)		(1000)		(1000)		(1000)		(1000)		(1000)		(1000)		(1000)
1	800	200	800	400	600	400	600	400	600	400	600	400	600	400	600
2	480	320	480	640	160	480	120	480	120	480	120	480	120	480	120
3	288	192	288	384	96	128	32	96	24	96	24	96	24	96	24
4	173	115	173	230	58	77	19	26	6	19	5	19	5	19	5
5	104	69	104	138	35	46	12	15	4	5	1	5	1	5	1
6	62	42	62	83	21	28	7	10	3	3	1	3	1	3	1
7	37	25	37	50	12	17	4	6	2	1	1	1	1	1	1
8	22	15	22	30	7	10	2	3	1	1	1	1	1	1	1
9	13	9	13	18	4	6	1	1	1	1	1	1	1	1	1
10 & older	21	5	21	10	3	3	1	1	1	1	1	1	1	1	1
		8		17	5	5	3	3	3						
Populations 2000			2000		1000		800		759		752		750		750
Deaths		1000		2000		1200		1041		1007		1002		1000	

It was shown under type I fisheries that the gear necessary to make a given catch varies inversely as the average population from which the catch is taken. If we were to assume that no natural mortality exists, all deaths being due to fishing, the quantity of gear necessary to produce a given mortality rate  $a$  would be proportional to catch/average population; or, from (33), to  $\frac{a}{1-a/2}$ . As an example, compare the two states of balance represented by columns 2-4 and 14-16, table II. For the first,  $a=0.4$ ,  $\frac{a}{1-a/2}=0.5$ ; for the second,  $a=0.8$ ,  $\frac{a}{1-a/2}=1.33$ . Thus to double the mortality rate it is necessary to increase the fishing effort by  $1.33/0.5=2.67$  times. In an actual fishery this relationship is somewhat complicated by the presence of natural mortality, whose effect may now be considered.

#### SEPARATING CATCH FROM NATURAL MORTALITY

Consider further the example of table II, dividing the mortality rates into their two components, natural and fishing mortalities. In the first situation

(columns 2 to 4) let the natural mortality rate  $=n=0.2$ , fishing mortality  $=m=0.25$ , their combined effect being  $a=0.4$ . In the second situation (column 6 and on), let the corresponding values be 0.2, 0.75 and 0.8. In the first situation the total mortality will be divided into catch and natural mortality in the ratio of 2.5 to 2; in the second situation, in the ratio of 7.5 to 2. From these the rate of exploitation or annual expectation of capture, is calculated in the first situation

$$\text{as } \mu = \frac{0.25}{0.45} \times 0.4 = 0.222; \text{ in the second as } \mu = \frac{0.75}{0.95} \times 0.8 = 0.632.$$

In table III, column 3, the catch in each year is segregated, and its relation to the average population on hand during the year is presented in column 5. (With a fixed fishing effort within each year, this latter has been found logarithmically, since the rate of decrease within the year will approach the exponential.) As in the last section, the ratio of catch to average population will be directly proportional to the fishing effort necessary to produce the rate of exploitation under consideration. Taking the first situation as unity, these are compared in column 6. It will be observed that to increase the rate of fishing mortality ( $m$ ) from 25 to 75 per cent, or by 3 times, an increase in gear of no less than 3.8 times will be necessary; while if it is desired to have the new rate in effect at once, in the first year of the change it must be 4.0 times what it was.

TABLE III. Catch statistics for the population of table II, given 20 per cent natural mortality rate, combined with a 25 per cent fishing mortality rate in the first year, and with a 75 per cent fishing mortality rate in subsequent years.

1	2	3	4	5	6	7
	Total mortality	Catch	Average population	Catch population	Relative gear in use	Relative catch/gear
1st year.....	1000	556	2000	0.278	1.00	1.000
2nd year.....	2000	1579	1414	1.117	4.02	0.707
3rd year.....	1200	947	894	1.060	3.81	0.447
4th year.....	1041	822	780	1.054	3.79	0.390
5th year.....	1007	795	756	1.052	3.78	0.378
6th year.....	1002	791	751	1.051	3.78	0.375
7th year.....	1000	790	750	1.051	3.78	0.375

A better comparison is of the rate of exploitation in the two cases: to increase the rate of exploitation ( $\mu$ ) from 0.222 to 0.632, or by 2.8 times, the gear must be increased by 3.8 times, or in the first year by 4.0 times.

This example illustrates the general law that to obtain a given increase in rate of exploitation, it is necessary to make a more than proportional increase in fishing effort. As a corollary, any given increase in gear will effect a less than proportional increase in rate of exploitation. Thompson and Bell (1934, p. 36) appear to have had an awareness of some kind of factor restricting the effectiveness of an increase in gear, though the one demonstrated above does not follow from their basic assumption of instantaneous recruitment. They were led to

propose tentatively the concept of competition between different units of gear, and set up a formula similar to (10) of this paper; but in a more recent paper (Thompson and Van Cleve 1936, p. 113) this proposal is repudiated, evidently because of the lack of any theoretical justification.

Speaking generally, then, the effect of an increase in gear will always be a less-than-proportional increase in the rate of exploitation (annual expectation of death by capture) in a type II fishery. Equally, a decrease in gear will produce a less-than-proportional decrease in rate of exploitation. It is interesting and useful to discover here a close parallelism between fisheries of type II and those of type I: with the latter also, an increase or decrease in gear produces a less-than-proportional effect upon rate of exploitation (figure 2). Moreover, as with type I, the greater the initial rate of exploitation, the less will it be increased by any given increase in effort. The similarity between the two types is in fact almost quantitative. In the example of table III, the final rate of exploitation calculable from equation (19), substituting  $\mu$  for  $m$ , is 0.613—compared to 0.632 obtained above. Similar close approximations, with errors not exceeding 7 or 8 per cent, are obtained for a wide range of values of  $\mu$ , and  $f_2/f_1$ , provided the natural mortality rate ( $n$ ) is not excessive—more than about 0.4. *Thus equation (19) and figure 2 have a certain value even in respect to type II fisheries*, for approximately calculating the new rate of exploitation which may be expected to follow change in effort. This correspondence will also facilitate treatment of the very large class of fisheries which combine the features of type I and type II to a greater or lesser extent.

The usefulness of this approximation is of course chiefly confined to cases where the rate of exploitation is known, for one year at least. Determination of this rate for type II fisheries will in general be more difficult than for type I fisheries, because of its more complex relationship to catch and average population. The only general method available appears to be the marking or tagging method, discussed earlier. We have not discovered any useful approximations by which catch and effort can be used to obtain an estimate of rate of exploitation in special cases, such as were discussed at some length under type I. Following any given change in gear, it is several years before accumulated stock can be removed, or replaced, so that catch per unit of gear only gradually reaches its new equilibrium value—a matter treated fully by Thompson and Bell (1934). If by chance gear remains constant for long enough periods to compare equilibrium values before and after a change, there is still a necessity for estimating natural mortality, before catch and catch-per-unit can be used to calculate rate of exploitation. And there will always in practice be considerable uncertainty as to whether or not recruitment is sufficiently uniform from year to year to make any calculation of this kind useful.

Failing any factual estimate of the rate of exploitation, the only possible procedure appears to be the setting up of trial estimates, deducing from figure 2 appropriate pairs of values of gear and exploitation rate, then by comparison with the observational data to weed out any obvious impossibilities. But the chances of obtaining the actual rate of exploitation with any useful precision in this manner do not appear to be great.

## CHANGE IN AVERAGE WEIGHT OF FISH

The foregoing has been concerned solely with population numbers. It frequently happens, however, that catch data are expressed in weight, rather than numbers. By sampling the catch the average weight of fish can be found in successive years and catch poundage converted to individuals, for the purpose of testing any hypothesis regarding the magnitude of the existing mortality rate and rate of exploitation. Weight data by themselves would be much harder to use for this purpose, because as mortality rate increases, the average size of fish caught decreases; hence the catch per unit of gear, in kilograms, will decline more rapidly than the same as number of individuals, after the first year of increased gear.

This may be illustrated with the example of tables II and III, assuming that the average weight of young fish caught during the first year is 1 kilogram, and that the average weight of the catch increases by 20 per cent per annum thereafter. The corresponding weights are plotted in table IV. The weight of fish caught per unit of gear, shown in the last line, declines in a manner similar to numbers caught per unit (cf. table III, column 7), but at the end is considerably lower, owing to the smaller average size of the fish. Of course a greater rate of growth of the fish would accentuate this decline, while a lesser rate would diminish it. We are not here directly concerned with the important question of what rate of exploitation will produce the greatest weight of fish caught, for various rates of growth—which was a subject of prime interest to such authors as Baranoff (1918), Thompson and Bell (1934), Graham (1938) and Russel (1939).

TABLE IV. Weight of all fish dying in successive years, of the population of table II, assuming a growth rate of 20 per cent per year; together with the weight of the catch, and the weight caught per unit of gear in use.

Year-class	Average weight	Successive years of fishing						
		3*	5*	7*	9*	11*	13*	15*
1st	1.000	200	400	400	400	400	400	400
2nd	1.200	304	740	576	576	576	576	576
3rd	1.440	276	553	184	156	156	156	156
4th	1.728	199	398	133	45	35	35	35
5th	2.074	143	286	95	31	10	8	8
6th	2.488	105	207	70	25	7	2	2
7th	2.985	75	149	51	19	5	3	3
8th	3.583	54	107	36	11	4	4	
9th	4.300	39	77	26	4	4		
10th	5.160	28	52	15	5	5		
Older	-	70	143	39	22			
Total fish dying, in kg.		1,571	3,140	1,675	1,275	1,180	1,154	1,157
Proportion caught		5/9	15/19	15/19	15/19	15/19	15/19	15/19
Weight of catch		875	2,480	1,322	1,007	922	920	915
Relative gear in use (table III)		1.00	4.02	3.81	3.79	3.76	3.76	3.76
Catch/gear		875	617	347	266	247	245	242
Relative catch/gear		1.000	0.707	0.398	0.305	0.283	0.279	0.277

\* These numbers are those of corresponding columns in table II



## APPLICATIONS TO EXISTING FISHERIES

In developing the theoretical treatment of both of the types of fisheries discussed above, it was necessary to postulate rather ideal combinations of population character and fishing methods. How far will these be of value in interpreting catch statistics of real fisheries? The answer to this question is, of course, peculiar to every individual fishery of which it may be asked, but a discussion of some points may be of value:

(1) A fishery attacks the population under consideration with unequal intensity in different areas.

For the purpose of the calculations given above it is important that fishing effort be approximately equally applied over the range that a species inhabits, so that the *a priori* chance of any fish being caught is approximately as great as that of any other of similar size and sex. If this is not true, serious errors may result. For example, an inshore fishery may catch, as one of its less important products, those individuals of a wide-ranging pelagic species which happen to be at the margin of the dangerous netted area. If the species is only feebly migratory at the time fishing is done, the fishing mortality among its inshore members may be quite severe, while that among the population as a whole is light. If it is desired to treat of the whole population, some method must be found of relating its abundance to that of the vulnerable fraction.

This example is a rather extreme case, but in practice it is probably only rarely that the whole of a population during any short interval is approximately equally vulnerable to fishing. On the other hand, if much gear is in use and if its location is frequently changed, it may in many cases be considered that for practical purposes the whole of the population has been equally exposed to capture.

A familiar miniature example of unequal vulnerability is the observation that a bottom-set gill-net, on the first night it is set in a particular location, will as a rule catch more fish than on succeeding nights. In this case the fish in the vicinity of the net are more vulnerable than those more remotely situated. The fishing mortality among the former group is naturally very high, so much so that one night's fishing catches a large fraction of their numbers.

(2) Different amounts of gear are used at different times during the fishing season; or the efficiency of the gear used varies within the season.

When either of these conditions occurs, with type I fisheries, the decline in the population due to fishing will not be of the uniform exponential type which forms the basis of the calculations given, but will be irregular. This will affect the validity of equation (19) to some extent. As long as the gear used at different times is more or less in the same proportion in successive years, this will probably not be an important source of error; though consideration should be given to its possible effect in each individual case.

If, however, the gear used at different times does vary from year to year, it will be difficult to compare the total fishing effort in the two years. An attempt at a correction compensating for this might be made by weighting gear in use at different periods by its efficiency then. The latter could be estimated from catch



per unit of gear at various times in a season when total fishing mortality is small.

In this paper up to this point gear has been considered as being in use continuously, so that the number of units (lines, hooks, traps, seines, feet of gill net, etc.) is a sufficient measure of fishing effort (subject to the various limitations discussed). But when there is any variation in the frequency with which it is set out, it will be more convenient to multiply gear in use by the time, or the number of times, it is set, which gives a measure of fishing effort in such units as number of seine hauls, foot-nights of gill net fishing, etc.

(3) When gear in use is increased, the additional units may occupy less favourable fishing grounds.

It is natural that, other things being equal, whatever fishing gear is in use should be set in the localities where it will catch most fish. If additional gear is put out, it may either itself occupy less favourable sites, or the whole fishery be forced to include a certain proportion of the less favourable locations. In either case, the increased amount of gear will not make the increase in catch to be expected of it, even during a short time interval.

Correction for a situation such as the above may be difficult, for it will not be easy to tell what weight should be given to it, unless catch statistics are available in such detail as to allow of a calculation of the relative productivity of different locations.

(4) When gear in use is increased, the additional units may increase the efficiency of all units, including what were there before.

Dr. J. L. Hart has suggested this possibility, pointing out that in fisheries attacking certain pelagic species, a larger number of vessels will facilitate locating the denser shoals of fish; so that, up to a point, all vessels will benefit from an increase in numbers.

(5) Complete extermination of the vulnerable part of a population, in a fishery of type I.

It is not probable that a commercial fishery will ever have a fishing mortality of unity, but this condition might obtain in a sport fishery, for a limited number of fish inhabiting a small body of water. In this case formula (19) will not always apply, as it is based on the assumption that there exists a sufficient approximation to infinite divisibility of the population being fished. In other words, if a given degree of fishing effort catches all the fish available, it will be impossible to *calculate* what smaller effort would produce a desired lesser degree of exploitation. The same will apply if a determination of mortality rate gives a result so great as to be indistinguishable from unity.

(6) Variations in annual recruitment, in a type II fishery.

Of all the simplifications necessary for the mathematical treatment of type II fisheries, that of uniform recruitment between years will perhaps be most often and most seriously at fault. The phenomenon of pronounced variation in numbers of successive age classes has been repeatedly demonstrated, particularly with clupeid fishes. Such changes in numbers of recruits tend to give values of catch per unit gear a variability that is largely unpredictable, and, in a type II fishery,

increase the difficulty of reducing data of catch and gear to terms of rate of exploitation. On the other hand, once a determination of rate of exploitation has been made experimentally, variable recruitment adds no new difficulty in the way of using figure 2 to calculate approximately its value for other fishing efforts.

(7) Change of natural mortality rate with age or size of fish, or size of population.

The discussion of type II fisheries was made on the assumption that mortality rates remain unchanged as the age of the fish increases. The introduction of mortality rates peculiar to each age brings no new principle into the calculations and does not materially change the conclusions derived.

More disturbing would be a change in natural mortality rate with population numbers—most probably taking the form of an increase in natural mortality rate as numbers increase. Such a condition would have the action of damping the effect of changes in fishing effort upon rate of exploitation, so that rate of exploitation would be more nearly uniform over any given range of efforts in use.

(8) Different susceptibilities of fish of different ages to capture.

Just as natural mortality rates probably differ with increasing age of the fish, so their vulnerability to the fishing gear may vary, and almost certainly in a different fashion. This will be true not only in the sense that very young fish will not ordinarily be caught, but variations will also occur among the fish ordinarily considered of commercial size, above all when very selective types of gear such as gill nets are in use. Introduction of variable rates of fishing mortality at different ages into a calculation like tables II and III will not, however, change the conclusions to be derived in any important respect, though the computation becomes considerably complicated. In particular, they do not invalidate the general principle that a change in rate of exploitation will tend to be less than proportional to a change in fishing effort. In one example which we worked out, allowing vulnerability to fishing to increase for the first, second, third, and subsequent year-classes in the ratio of 1:2:4:5, the average rate of exploitation following an increase of gear was within 5 per cent of what was calculated from figure 2. It should be noticed that the procedure followed in table II, of assigning one-half the regular mortality rate to the incoming year class, can be regarded as a somewhat special case of the general phenomenon of reduced rates of fishing mortality upon the younger age groups.

The points above by no means exhaust the number of ways in which a real fishery may differ from the ideal ones described in this paper. It will probably never be an easy task to check the abundance, or the rate of exploitation, of a large fish population by means of statistics of catch and gear. The collection of the necessary statistical information is itself usually difficult enough, requiring the assistance of many individuals. When these data are obtained, there are problems of equating different types of gear, of determining the relative efficiency of the gear for fish of different sizes (which is important when the size composition of the population changes from year to year), or of deciding the effect upon vulnerability, of any observed change in body proportions of the populations.

Another group of errors may arise from the operation of any factors which affect the random capture of fish by the nets. As an example may be mentioned the much-discussed possibility that when a gill-net has caught a certain number of fish, the line of dead bodies may cause others to avoid it, so that until it is cleared it is in effect no longer fishing. A useful discussion of some of the difficulties encountered in this work is given by Van Oosten (1936).

Additional sources of error will occur in great variety to every student of this subject. One piece of encouragement may be held out: it is most unlikely that all such discrepancies should tend to weight the results with cumulative errors in the same direction; but it is quite possible that they may cancel each other's effect to such an extent that unadjusted or "raw" data will conform reasonably well to a simple theoretical treatment.

### SUMMARY

1. For purposes of mathematical analysis, human exploitation of animal populations may conveniently be divided into two main types: I,—those cases where, while it persists, the mortality inflicted by man is so much greater than the balance of natural mortality and recruitment that these last can be ignored; II,—those cases where natural mortality and recruitment must be considered to take place uniformly and simultaneously with man's toll.

2. In fisheries conforming to type I, the relation between fishing effort and rate of exploitation (annual expectation of death by capture) is expressed by the logarithmic curves of figure 2. The same figure expresses *approximately* the relation between effort and rate of exploitation in most type II fisheries, and presumably also many intermediate types. In either case change in fishing effort produces a less-than-proportional change in rate of exploitation; the effect of a change being the less, the greater is the initial rate of exploitation. There is no general method by which rate of exploitation can be determined from statistics of catch and gear, although a satisfactory application of Peterson's marking technique will provide this information experimentally.

3. In both types of fisheries catch per unit effort is a valid estimate of the relative size of average populations on hand *during the fishing season* of successive years. In certain special cases of type I fisheries it can be used also to obtain a relative measure of initial population, and hence used to follow secular changes in abundance from year to year. In other special cases of type I, the exploitation rate, and hence the absolute number of individuals in the population, can be calculated from values of catch and effort, particularly if data for a series of years are available.

4. Many difficulties may arise in determining from the records of gear in use, the actual fishing effort applied in successive years. These and other obstacles to a theoretical treatment of statistics of catch and gear are briefly discussed.

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Preparation of the manuscript was begun in 1935 and continued, with one major interruption, down to the winter of 1939. Much additional material could profitably be added to the paper. It is presented in its present form partly to keep its size within bounds, partly in response to requests that it receive an early publication.

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## Embryonic Developmental Rates and Egg-Laying of Canadian Lobsters

BY W. TEMPLEMAN

*Memorial University College, St. John's, Newfoundland*

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### ABSTRACT

The comparative times required for similar lobster eggs already slightly developed, to reach the 16-cell stage, at 18.5, 14.4, 12.3, 10.5, 9.9, and 4.7° C. are 2, 3, 3.6, 4.8, 5.6 and 25 days respectively.

Egg-laying is almost a month later at Grand Manan than in the warmer southern gulf of St. Lawrence areas. Egg-laying in the southern part of the gulf of St. Lawrence takes place in two bursts, the first being egg-laying by old-shelled lobsters usually occurring in the latter half of June and in July, and the second, egg-laying by new-shelled lobsters occurring mainly in August in the warmest areas.

Female lobsters rarely lay eggs before becoming hard-shelled. Development of the lobster egg usually requires 11½ to 12 months in Canadian waters.

### RATE OF DEVELOPMENT AT VARIOUS TEMPERATURES

#### TO 16-CELL STAGE

During the summer of 1935 at the Biological Station at St. Andrews, N.B., we were fortunate in observing a lobster laying eggs. Egg-laying, which lasts several hours, was completed at 4.35 p.m., July 18. After egg-laying the eggs are at first flattened and cannot be handled. The newly berried lobster therefore was kept in a running-water tank at a temperature of 12.0°C. until 9.40 p.m., July 19. At 10.00 p.m., July 19, eggs were removed from the lobster and placed in wide-mouthed pint bottles half full of sea water. About a dozen eggs were placed in each bottle, and the bottles kept at different temperatures. Observations were taken from time to time to determine when the eggs at each temperature reached the 16-cell stage. A graded series of temperatures from 1°C. to 18.4°C. was obtained by using an insulated box divided into chambers and with ice at one end and electric lights and a De Khotinsky regulator at the other. The results for some of these temperatures were roughly checked by control bottles placed in various parts of the laboratory where temperatures were fairly constant throughout the day, and an additional check was provided by allowing the berried lobster from which the eggs used in the experiment were taken to remain in the running water tank. Large numbers of eggs were left attached to the lobster and the state of development of these eggs was noted from day to day. The sea water in the bottles was replaced by water raised or lowered to the appropriate temperature daily at the higher temperatures and

every second or third day at the lower temperatures. The bottles were shaken daily to change the position of the eggs, and daily temperature readings were taken. At the higher temperatures the eggs were examined daily, at 4.7°C. every two days and at 1°C. every week. The data given in figure 1, therefore, have a possible error of a few hours. Since at the lower temperatures it was impossible to examine the eggs even rapidly under the microscope without raising the temperature somewhat the lobsters at lower temperatures were not examined under the microscope until the eggs at the temperature several degrees above had reached the 16-cell stage. At all temperatures from 4.7 to 18.5°C. the eggs remained healthy and developed in a normal fashion considerably beyond the 16-cell stage. Eggs remaining attached to the lobster in running water had a rate of development which fitted the curve of development at various temperatures in the bottles (see figure 1). It is highly probable,

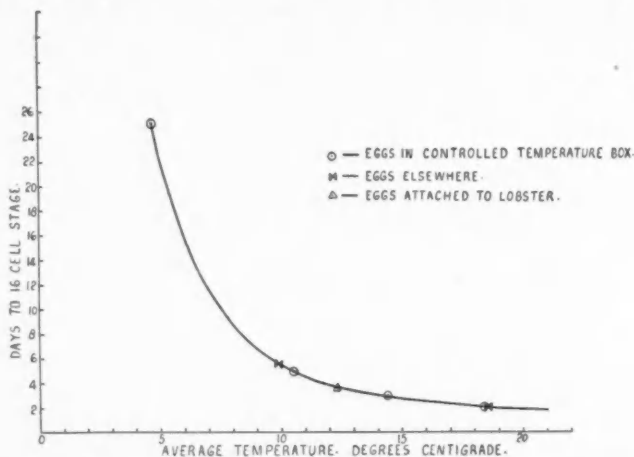


FIGURE 1. Time for development to the 16-cell stage at 4.7 (4.3-5.5), 9.9 (9.6-10.2), 10.5 (10.3-10.6), 12.3 (12.2-12.3), 14.4 (14.2-14.5), 18.4 (constant), 18.5 (17.7-19.2°C.).

therefore, that the rate of development of the lobster egg at various temperatures obtained in our experiments and shown in figure 1 is approximately correct.

As shown in figure 1, the lobster egg after developing at 12.0° for 1 day and 5 hours after egg-laying, developed to the 16-cell stage in 2 days at 18.5°, in 3 days at 14.4°, in 3.6 days at 12.3°, in 4.8 days at 10.5°, in 5.6 days at 9.9° and in 25 days at 4.7°C. At 1.0° (range 0.7 to 1.8) the eggs remained healthy for 58 days with no indication of cell division, and the experiment was then discontinued.

#### TO EGG NAUPLIUS AND EYE-PIGMENT STAGES

Herrick (1896), at Woods Hole, studied the rate of egg development, the lobster eggs remaining attached to the lobster at 21° (20 to 22°C.). In the

development of the lobster egg there are certain very definite stages such as the egg-nauplius stage and the first appearance of the eye pigment. In figure 2 Herrick's observations on the length of time required after egg laying to reach the various stages of egg development at 21°C. are represented in a straight line graph for comparison with results obtained at lower temperatures by the author. At St. Andrews in July and August, 1934 and 1935, lobsters were carefully watched for egg-laying and three lobsters with eggs unsegmented, which had laid eggs not more than 1 to 3 days previously, were tagged with numbered metal tags. These lobsters were then returned to tanks containing running sea water in dim light, and samples of the eggs were taken from time to time to determine the development. In the case of lobster A (figure 2) egg-laying was

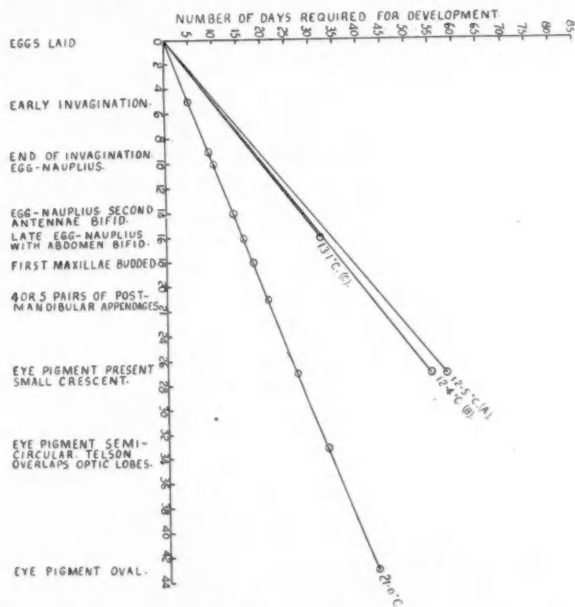


FIGURE 2. Time for development to egg-nauplius and eye-pigment stages at low temperatures compared with same to various stages at 21°C. in Herrick's experiment.

actually observed and in the cases of lobsters B and C (figure 2) the date at which the eggs reached the 16-cell stage was observed and the date of egg-laying calculated from figure 1.

The eggs from lobster C at 13.1° required 32 days after egg-laying to reach the late egg-nauplius stage, as compared with 16 days in the case of Herrick's experiments at 21°. Lobster A at 12.5° and lobster B at 12.4° required 58 and 55 days respectively to reach the stage at which eye pigment first developed, as compared with 27 days in the case of Herrick's experiments at 21°C.

These results obtained at St. Andrews are accurate to within a day in lobsters A, B, and C, since there could be no greater error than this in determining the date of egg-laying.



TABLE I. Comparison of times for early and later development of the lobster egg at various temperatures (data from figures 1 and 2 and from Herrick 1896\*). Figures in brackets represent the ratio of development at the various lower temperatures to that at 21° when Herrick's figures have been increased by 1 day.

Temp. (°C.)	Days to reach			Relative time (at 21°C. = 1) to reach		
	16-cell stage	Late egg-nauplius stage	Eye-pigment stage	16-cell stage	Late egg-nauplius stage	Eye-pigment stage
12.45	3.6		56.5	2.00		2.09 (2.02)
13.1	3.3	3.2		1.83	2.00 (1.88)	
13.7	3.1			1.72		
21.0	1.8	16*	27*	1	1*	1*

Table I shows the time required for egg development to various stages assuming the time taken at 21°C. to be 1. It is seen that if it is assumed that Herrick's figures for the various stages are 1 day too little, the rate of development to the 16-cell stage at various low temperatures is approximately the same compared to that at 21° as the rate of development to the egg-nauplius and eye-pigment stages at these low temperatures. (It is most probable that Herrick's figures are over a day too low, since Herrick through his failure to observe the exact time his lobsters laid eggs estimates that 32 yolk segments are present about 28 hours after egg-laying and fertilization, whereas according to our own calculations it would require about 2 days and 10 hours after completion of egg-laying for the 16-cell stage to be reached at 21°C.).

Since the rates of development to the 16-cell and later stages are approximately the same at the same temperature (table I), we have used the rates of development in figure 1 to the 16-cell stage at different lower temperatures as compared with development at 21°, and from this calculated when the later stages such as egg-nauplius, eye-pigment, etc., would be attained, using as a basis of calculation Herrick's (1896) figures for these stages at 21°C.

#### EGG-LAYING

The dates of egg-laying in various areas were calculated by examining samples of "new" or freshly laid eggs obtained in 1931, 1932, 1936 and 1937. Most of these eggs had been extruded less than a month, and nearly all the remainder less than two months previously.

There is a long developmental period in the lobster egg, the female carrying the eggs attached to her swimmerets for about eleven to twelve months before hatching, and the early stages occurring for several months after egg-laying are well marked. Changes in the egg can be noted by superficial examination, almost daily during the first month and every few days during the second. The stage of development of the egg samples was determined, using as a standard the rate of development of eggs at Woods Hole, July 9 to September 1, 1890,



given by Herrick (1896). The temperature at which development took place at Woods Hole from July 9 to August 12, ranged from 20 to 22° and averaged 21°. Temperatures later than August 12 were not recorded. It is assumed that these later temperatures during August and the first week or two of September did not vary much from 21°C.

Using figure 1 showing the rate of development of the lobster egg to the 16-cell stage at different temperatures in conjunction with Herrick's standard of development for the first two months at 21°, the number of days elapsing since egg-laying was calculated at the temperature prevalent in the particular area during the early development of the egg.

The term "berried lobster" often used in the discussion refers to a female lobster carrying external eggs attached to her abdomen.

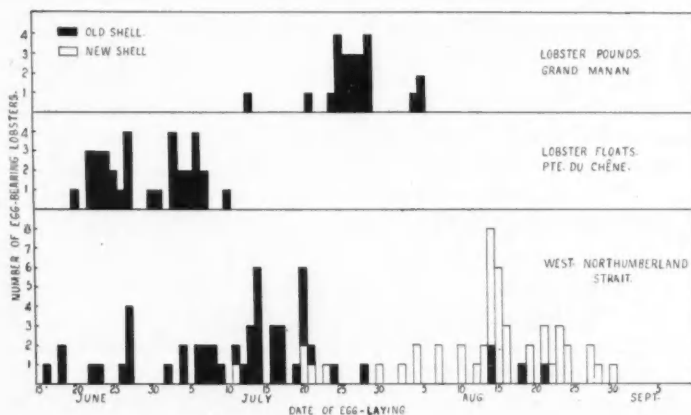


FIGURE 3. Calculated dates of laying for new eggs collected August 4 to 14, 1932, at Whitehead and Woodward's cove pounds, Grand Manan; June 27 to July 11, 1932, from Paturel's lobster floats at Pointe du Chêne; and August 31 to September 19, 1932, from Western Northumberland strait.

#### DATES IN WARM AND COLD AREAS

Figure 3 gives a comparison of the calculated dates for the beginning of egg-laying in the lobster floats at Pointe du Chêne, N.B., in the lobster pounds at Whitehead and Woodward's cove, Grand Manan, and on the lobster fishing grounds in western Northumberland strait in 1932. Thirty-four samples of new eggs were obtained from the lobster floats at Pointe du Chêne from June 27 to July 11, the calculated dates of egg-laying, according to the rate of development at 18.0° (0.86 times the rate at 21°) ranging from June 20 to July 10. (Temperatures at the bottom of the floats from June 28 to July 11 ranged from 16.8 to 21.1° with an average daily temperature of 18.0°). The lobsters in these floats had been brought before June 30 from point Sapin, about 84 kilometres north of Pointe du Chêne and from the western shore of Prince Edward Island nearby. In the Whitehead and Woodward's cove pounds, Grand Manan, the

egg samples from 23 new-egg lobsters were collected between August 4 and 14. The lobsters from which the eggs were collected in these pounds had been obtained during the spring season at least several months previously from Grand Manan and southern Nova Scotia (from Clarkes harbour west). The bottom temperatures in these pounds obtained on August 3, 5, 12, 13, 16 and 18 ranged from 11.0 to 11.9° with an average temperature of 11.5°. The dates of egg-laying of these lobsters were therefore calculated, using the rate of development of the lobster egg at 11.5° (0.43 times the rate at 21°C.).

The berried lobsters collected from the Whitehead and Woodward's cove pounds according to these calculations laid eggs between July 13 and August 5, only 1 of the 23 lobsters having laid eggs before July 21.

Both in the floats at Pointe du Chêne and in the pounds at Grand Manan the eggs had been laid only a few (usually less than ten) days before collection, and the developmental temperatures used are approximately correct. Therefore the calculated dates of egg-laying shown for these areas must be correct within a day or two.

Egg-laying in the Grand Manan region, therefore, is roughly about a month later than on the southern gulf area owing presumably to the considerably lower summer water temperatures at Grand Manan.

#### BY NEW- AND OLD-SHELLED LOBSTERS

Figure 4 shows the calculated time of egg-laying and the condition of shell of newly berried lobsters from egg samples collected in western Northumberland strait in 1931 and 1932 at Pointe du Chêne and Summerside, and in 1936 and 1937 at Pointe du Chêne. There was no selection of berried lobsters for shell condition, egg samples having been taken partly from berried lobsters normally found in the fishermen's catches, in which case the lobsters would be those which the fisherman had failed to return to the sea, and would mostly consist of the smaller berried lobsters. The remainder of the egg samples, 45% in 1931, 92% in 1932, 85% in 1936 and 95% in 1937 were obtained in cases where the fisherman brought his whole catch of berried lobsters ashore for examination, egg samples being taken from all the berried lobsters. The shell condition was recorded, without reference to the stage of development of the eggs when the egg sample was taken, and the stage of development of the eggs was determined several months later.

#### STANDARD OF DEVELOPMENT

In 1931 in western Northumberland strait the egg samples were collected from August 19 to September 17, in 1932 from August 31 to September 19, in 1936 from August 20 to 24, and in 1937 from August 17 to September 4.

For western Northumberland strait Bjerkan (1919) gives temperatures at Station 28 (approximately in the middle off Pointe du Chêne) as being from 17.1° at 10 metres to 17.0°C. at 20 metres at noon on August 3, 1915. Our observations near Medea rock in Shediac bay in 1932, for depths of from 7½ to 9 metres gave bottom temperatures ranging from 13.2 to 16.1°C. for the

period July 4 to 18. Mr. J. W. Fisher's observations in 1932 for a station two miles northeast of Pointe du Chêne, with a depth of 5 metres, gave bottom temperatures ranging from 14.6 to 22.0°C. for the period June 18 to September 9.

No single standard of development will be correct for both offshore and inshore or for different years, and we have adopted the compromise of using the rate of development at 19°C. for August and early September, and for July and June the rate of development at 16°. According to figure 1 the rate of development at 19° is 0.93 that at 21°, and at 16° is 0.71 that at 21°C.

Lobsters whose eggs developed in warm coves or harbours would by these standards be calculated to have laid eggs a few days earlier and lobsters whose

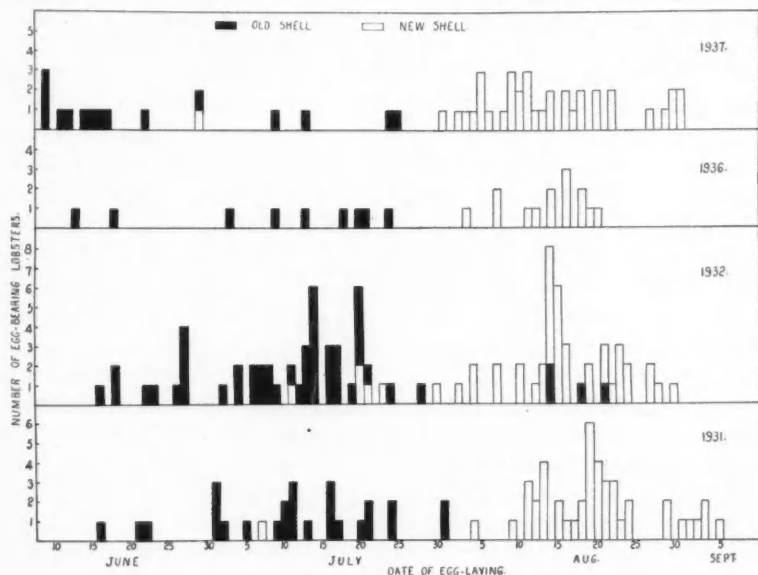


FIGURE 4. Calculated dates of laying for new eggs from old and new-shelled lobsters collected in Western Northumberland strait from August 19 to September 17, 1931; from August 31 to September 19, 1932; from August 20 to 24, 1936; and from August 17 to September 4, 1937.

eggs developed in the middle of the strait in 20 metres or more would in figure 4 be shown laying eggs a few days later than the actual date of egg-laying. Such errors, however, are very small in the case of the new-shelled lobsters which laid eggs only a few days or weeks previous to the collection of the egg samples. Even in the case of lobsters laying eggs several months before the collection of the egg samples the calculated date of egg-laying can hardly be more than a week from the correct date, since in figure 3 the calculated date of the first egg-laying in nature in western Northumberland strait is June 16 while the earliest calculated date of egg-laying in the floats at Pointe du Chêne is June 20. These latter lobsters were originally obtained from regions immediately neigh-

bouring to western Northumberland strait, the daily temperatures in the floats were known, the rate of development calculated accordingly and the eggs had been laid only a few days before collection. The calculated dates of egg-laying in these floats, therefore, are correct; at least the error cannot be greater than a day or two.

The calculated dates for 1937 are possibly more incorrect than in other years since the water in western Northumberland strait was exceptionally warm in this year, temperatures as high as 24°C. being attained in late August in the lobster floats at Pointe du Chêne. If, as is possible, the standards of development used are too low for this year, the egg-laying calculated for 1937 (earliest June 9) may be a week too early.

#### TWO BURSTS

In 1931, 1932, 1936 and 1937 egg-laying in western Northumberland strait took place in two bursts, the first being egg-laying by old-shelled lobsters which had not moulted since the previous year and usually occurring during the latter half of June and in July, and the second, egg-laying by new-shelled lobsters occurring mainly in August, these new-shelled lobsters having moulted earlier in the same summer that the eggs were laid. On the average the old-shelled lobsters spawn about a month earlier than the new-shelled lobsters. The occasional new-shelled lobsters recorded as extruding eggs early in July may be due to failure to determine the shell condition properly in a few cases, a very clean fresh-looking old-shell from deep water possibly being called new-shell.

In the four years mentioned above 99 old-shell and 141 new-shell lobsters with new eggs were obtained. It is difficult, however, to estimate the true percentage of lobsters laying eggs in the old and in the new-shelled condition since the new-shelled lobsters would probably be feeding better and trapping more readily than the old-shelled.

#### END

As shown by figure 4, there is relatively little egg-laying during September in western Northumberland strait. In 1931 when egg samples were collected between August 19 and September 17 a few lobsters obtained from the colder deep water off Summerside extruded eggs in early September; in 1932, however, when all the egg-samples from western Northumberland strait were collected after August 30 and 64 per cent between September 14 and 29, the latest calculated date of egg-laying was August 30.

In eastern Northumberland strait with its lower bottom temperatures (Bjerkkan 1919) there is apparently considerable egg-laying in September. Knight (1917) records that of 50 female lobsters placed in two pens at Bay View on the southern side of eastern Northumberland strait on August 30, 1916, 13½ per cent had laid eggs by September 30.

#### OTHER AREAS

Egg-laying in both the old and the new-shelled conditions occurs also at the Magdalen islands, where in 1931 two old-shelled lobsters with new eggs were caught on July 20 and July 25 respectively during experimental fishing in Pleasant bay, and a new-shelled lobster with new eggs was caught in House harbour lagoon on August 6, this lobster having extruded eggs about August 4.

In eastern Northumberland strait also the same phenomenon occurs, undoubted old- and new-shelled lobsters being found with new eggs in a catch of lobsters from off Victoria harbour on September 21, 1932. The two new-shelled berried lobsters found in this case were 27 cm. long, possessed hard-buckle shells and had moulted probably not more than a month previously.

Examination of ten berried lobsters with old eggs at Grand Manan from May 31 to June 3, 1932, and eight others in June 1933 showed that all these possessed shells at least a year older than most non-berried females in the same area. The mature females in this area are very large and our data indicate that moulting would take place in September or even later among these large sizes. Berried lobsters as a rule require a period of several weeks or more after moulting for hardening of the shell before the eggs are extruded, so that in the Grand Manan area the temperature may be lowered so much by the time moulting and the subsequent hardening of the shell by these large females has been completed that few if any new-shelled lobsters lay eggs.

#### EXPERIMENT WITH NEW-SHELLED LOBSTERS

As a check on our determinations of shell condition in berried lobsters with new eggs, 42 definitely new-shell hard-buckle shell mature female lobsters without external eggs were selected from the fishermen's catches at Pointe du Chêne on August 14, 1937, isolated in a compartment of a lobster float at Pointe du Chêne, and fed daily. All of these lobsters had definitely moulted in 1937, the moulting period of these larger lobsters at Pointe du Chêne being about the middle of July. When the lobsters were examined again on September 4, twelve were carrying new eggs.

#### DAWSON'S OBSERVATIONS

Since the distinction between new-shelled and old-shelled lobsters depends on personal judgment it is most definite during the moulting season, in the summer, when all stages of old-shell, moulting and new-shelled lobsters are present. Dawson (unpub. MS.), who carried on experimental fishing at Cape Traverse in the intermediate region between western and eastern Northumberland strait from June 24 to September 12, 1918, during which time 386 berried lobsters were caught, says: "The first new or green eggs were found on July 12. Up to August 27 all the females with freshly extruded eggs were hard-shelled, and old-shelled. On August 27 a small 8 inch female with a new shell and bearing new eggs was taken and within a few days the numbers of 'hard-' and 'soft-shelled' lobsters with new eggs became approximately equal."

## HARDNESS OF SHELL

Shells of old-shelled female lobsters with new eggs are of course extremely hard since these lobsters have not moulted for a year or more.

Female lobsters rarely lay their eggs before the lobster has recovered somewhat from moulting and the new shell has become hard. Thus of 57 new-shell new-egg lobsters examined in 1931 in Northumberland strait, only two were buckle-shelled, the remainder being hard-shelled. Of 60 new-shell new-egg lobsters examined in the same area in 1932, two were hard buckle-shelled, the remainder being hard-shelled. Many of these lobsters had laid eggs only a few days previously. To illustrate the difference in shell condition between berried and non-berried females, in western Northumberland strait from August 19 to 26, 1931, from a total of 32 new-shell new-egg lobsters, only 2 or 6 per cent were buckle-shelled, the remaining 94 per cent being hard-shelled. In the same area on the same dates, out of 1534 new-shell non-berried female lobsters above 22 cm. (mature size), 22 per cent were rubber-shelled and 44 per cent buckle-shelled. Thus practically all the females reach the hard-shelled condition before laying eggs. The time required for a mature female lobster to reach the hard-shelled condition in this area after moulting would be about three to six weeks, depending on size. Thus, since non-moulting, old-shelled lobsters mainly lay eggs during the moulting period of the year, among the mature moulting lobsters maximum egg-laying is after moulting and about a month later. If moulting is early, as in western Northumberland strait (Templeman 1936), new-shelled lobsters have recovered from moulting sufficiently to lay eggs in early August. If moulting is later, as almost certainly occurs in the colder parts of eastern Northumberland strait, egg-laying by new-shelled lobsters is later, and if moulting is very late as at Grand Manan where moulting of mature females occurs in September and possibly later, few or no new-shelled lobsters lay eggs.

## LENGTH OF EMBRYONIC PERIOD

## WESTERN NORTHUMBERLAND STRAIT

According to records of first appearance of fry in lobster hatcheries at Buctouche and Shemogue between 1906 and 1917 (Templeman 1936), the earliest hatching in western Northumberland strait usually occurs about June 10. It is unlikely that the date of natural hatching is more than a day later than this, since the first eggs were usually placed in the above hatcheries about the last of May and a continuous supply of sea water was always running through the jars containing the eggs. In Dawson's experimental fishing at cape Traverse in 1918 (unpub. MS.) hatching fry were first observed on June 21. Since the cape Traverse region is intermediate between western Northumberland strait and the colder eastern Northumberland strait, and many warmer areas exist in the western part of the strait, the period June 10 to 15 can be regarded as the probable date for the beginning of natural hatching in this area. It must be remembered also that from the time a lobster begins hatching it takes from one to two weeks for all its eggs to hatch out.

With regard to the end of the hatching period in western Northumberland strait, the author (Templeman 1936) gives evidence to show that in western Northumberland strait hatching is nearly over by the first of August, probably over 90 per cent of the berried lobsters having hatched by this time, and that hatching in this area is certainly completed by August 20 except in the intermediate deep, colder water area between cape Tormentine and cape Traverse.

From figures 3 and 4 egg-laying in western Northumberland strait usually begins about June 15 and is mainly completed by the end of August. The eggs are therefore usually carried by the female lobsters in this area for a period of about  $11\frac{1}{2}$  to 12 months.

#### EASTERN NORTHUMBERLAND STRAIT

In 1916 at the Bay View lobster hatchery near Pictou in eastern Northumberland strait, Professor MacClement first noted that new eggs were being brought to the hatchery about the middle of June. Mr. A. B. Dawson examined on June 23, 24 and 27, 93 berried females brought to Burnham and Morrill's lobster factory at Bay View and of these, 15 bore new eggs (Knight 1917). In 1916 at Bay View eggs were placed in the hatchery from early May onward and the first hatching occurred in the week of June 25 to 31, the average date of first hatching in Bay View hatchery in 9 years between 1906 and 1917 being June 21. There are, therefore, about 12 months between earliest egg-laying and earliest hatching at Bay View.

#### GRAND MANAN AREA

The water around Grand Manan possesses a much lower summer temperature than that of western Northumberland strait. Temperatures during the winter, however, are slightly higher at Grand Manan (Templeman 1936).

In 1933 eight berried lobsters were trapped at Grand Manan and transferred to running water tanks at St. Andrews on June 10. On July 27 the first fry were hatched from one of these lobsters. On August 6 this female had almost completely hatched, another was hatching and 6 had not yet begun hatching. By August 14 five females had completed hatching, two were hatching and one had not yet started. The last female completed hatching on August 23. The temperatures in the tanks at St. Andrews from June 12 to August 15 ranged from  $10.4^{\circ}$  to  $14.1^{\circ}\text{C}$ . These temperatures are several degrees higher than the Grand Manan lobsters would have experienced during the same period on their natural grounds, so that calculating from figure 1 the above dates are at least a week too early.

In figure 3 the earliest egg laying among the 23 berried females examined from the lobster pounds at Grand Manan was July 13 with little occurring before July 21. These data, although limited, render it probable that the eggs in this area have a developmental period of twelve months or even slightly longer.



## OTHER AREAS

Herrick (1896 and 1911) says that the developmental period of the eggs on the coast of Massachusetts occupies approximately ten and a half months. The one berried lobster cited by Herrick, however, which was kept under observation at the Fish Commission station at Woods Hole, began to hatch in 334 days, or 11 months after egg-laying, the eggs being laid on July 1, 1890, and hatching beginning on June 1, 1891. Since it takes a lobster one or two weeks to complete hatching, this lobster would only have completed hatching in  $11\frac{1}{4}$  to  $11\frac{1}{2}$  months after egg laying.

The author (Templeman 1939) has shown that on the west coast of Newfoundland in 1938 hatching was beginning during the last week of June, and out of 27 berried lobsters with new eggs caught in special fishing in St. Georges bay between July 20 and August 20, one lobster had laid eggs on July 6 and the next on July 15. In this area, therefore, the developmental period is about  $11\frac{1}{2}$  months.

## SUMMARY

The lobster egg after developing at  $12.0^{\circ}\text{C}$ . for 1 day and 5 hours after egg-laying developed to the 16-cell stage in 2 days at  $18.5^{\circ}$ , in 3 days at  $14.4^{\circ}$ , in 3.6 days at  $12.3^{\circ}$ , in 4.8 days at  $10.5^{\circ}$ , in 5.6 days at  $9.9^{\circ}$  and in 25 days at  $4.7^{\circ}$ . At  $1.0^{\circ}\text{C}$ . the eggs remained healthy for 58 days with no indication of cell division.

At  $13.1^{\circ}$  the lobster egg required 32 days after egg-laying to reach the late egg-nauplius stage as compared with 16 days at  $21^{\circ}$ . At  $12.45^{\circ}$  the lobster egg required  $56\frac{1}{2}$  days to reach the stage at which eye-pigment first developed as compared with 27 days at  $21^{\circ}\text{C}$ .

Egg-laying in the lobster floats at Pointe du Chêne in 1932 began about June 20, while in the colder water of the lobster pounds at Grand Manan the first eggs were laid about July 13, only 1 in 23 lobsters laying eggs before July 21.

In the four years in which investigations were carried on (1931, 1932, 1936 and 1937) egg-laying in western Northumberland strait took place in two bursts, the first being egg-laying by old-shelled lobsters usually occurring during the latter half of June and in July, and the second, egg-laying by new-shelled lobsters occurring mainly in August. In the above four years 99 old-shell and 141 new-shell lobsters with new eggs were collected.

Egg-laying in both the old and the new-shelled conditions occurs also in the Magdalen islands and in eastern Northumberland strait, but probably egg-laying in the new-shelled condition does not occur at Grand Manan.

Very little egg-laying occurs in western Northumberland strait in September, but in eastern Northumberland strait with its colder bottom water there is considerable egg-laying in this month.

Female lobsters only rarely lay their eggs before they are hard-shelled, and the late moulting with slow recovery in cold water regions such as Grand Manan prevents new-shelled lobsters from laying eggs in these regions.

The development of the lobster egg from egg-laying to hatching occupies about  $11\frac{1}{2}$  to 12 months in western Northumberland strait, and about 12 months in the lower water temperatures at Grand Manan.



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# Factors Limiting Distribution and Size in the Starfish

BY G. F. M. SMITH,  
*Atlantic Biological Station*

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## ABSTRACT

In shallow water of Malpeque bay, P.E.I., the distribution of the starfish *Asterias vulgaris*, Verrill, is limited by temperatures over 25° C. in the summer and salinities less than 14 per mille in the winter. Small starfish have a higher temperature tolerance than large starfish. The population on denuded areas is replaced by the immigration of adults and the settlement of larvae. The maximum distance travelled by a marked starfish was 200 metres and the average about 20 metres, in four months. Starfish move directly towards food a distance of 12 metres at 6 metres per day. The maximum population density found was 60,000 per acre (15 per sq. metre) and the greater the population density, the smaller the modal size. Rate of growth varies with the kind and abundance of food and inversely with the size of the starfish. Spawning takes place in late May and early June and the larval life is about three weeks.

## INTRODUCTION

The starfish is a common pest on oyster beds and in some places large quantities of oysters are devoured by starfish. It has been usual procedure to remove the starfish by mechanical means. With the point of view of the commercial oyster fishery in mind, it was thought advisable to investigate some of the factors that limit or affect the distribution and the size of the starfish.

Galtsoff and Loosanoff (1939) published the results of an extensive study on the natural history of *Asterias forbesi*, Desor. Although the present study is on a different species, the work is for the most part complementary as method of attack and point of view differ.

The experimental and observational work was mostly confined to part of Malpeque bay on the north side of Prince Edward Island, in the gulf of St. Lawrence.

The only species of starfish that occurs on oyster areas in eastern Canada, in significant numbers, has been identified as *Asterias vulgaris*, Verrill.

## METHOD OF CAPTURE

The gear used to obtain starfish samples from oyster beds, and to estimate population density on areas of bottom (by removing as many starfish as could be caught), was a set of tangles of cotton waste or mops, that were fastened to a heavy iron triangle and towed over the bottom by a motor boat at reduced speed. It was noticed that the gear was inefficient in capturing starfish of the

current year, as individuals less than one centimetre in diameter do not frequently become entangled in the threads of the mops. On this basis it might be reasonable to doubt the efficiency of the gear, when it is used to estimate the total number of starfish on an area of bottom.

Two short experiments were carried out to test the efficiency of mops in catching starfish of the sizes most frequently obtained by the method. The technique employed was to mop up a number of starfish, stain them with Nile blue, place them back on a known area of bottom and attempt to recapture them with the same mops.

In the first experiment, 1,600 stained starfish were placed on an area of about  $1/20$  acre (200 sq. metres) of hard bottom. In the first  $2\frac{1}{2}$  hours mopping, over 50%, and in 12 hours, 72% were recaptured (table I). In the second

TABLE I. Recaptures from 1,600 stained starfish on  $1/20$  acre (200 sq. m.) by successive moppings

Mopping time (hours).....	$2\frac{1}{2}$	$2\frac{1}{2}$	2	3	2
Cumulative total time.....	$2\frac{1}{2}$	5	7	10	12
Starfish (number).....	827	161	119	33	12
Cumulative percentage.....	52	62	69	71	72

experiment, 3,200 were placed on 1 acre (4000 sq. metres). In the first three hours, 31%, and in 28 hours, 86% were recaptured (table II). In both experiments

TABLE II. Recaptures from 3,169 stained starfish on 1 acre (4,000 sq. m.) by successive moppings

Mopping time (hours).....	3	$1\frac{1}{2}$	3	$1\frac{1}{2}$	3	$2\frac{1}{2}$	1	$1\frac{1}{2}$	$1\frac{1}{2}$	$3\frac{1}{2}$	$3\frac{1}{2}$	2
Cumulative total time.....	3	$4\frac{1}{2}$	$7\frac{1}{2}$	9	12	$14\frac{1}{2}$	$15\frac{1}{2}$	17	$18\frac{1}{2}$	22	$25\frac{1}{2}$	$27\frac{1}{2}$
Starfish (number).....	978	439	512	162	208	142	28	52	25	89	79	15
Cumulative percentage.....	31	45	61	66	73	77	78	79	80	83	85	86

the percentage of starfish recaptured approached a level significantly less than 100%. The data were found to fit an equation of the form

$$N = K(1 - e^{-rT})$$

where  $T$  is the mopping time,  $N$  is the percentage recaptured at any time ( $T$ ),  $K$  is the asymptote of the curve and the percentage that would be recaptured if mopping were continued for an indefinitely long (infinite) time,  $r$  is the rate of recapture and  $e$  is the base of natural logarithms.

The above equation fitted to the data of both experiments (figure 3), accounts for 99% of the stained starfish at the time the mopping operations

were stopped. In each experiment mopping was continued until the catch in the last hour was less than 2% of the catch in the first hour.

Towing the heavy iron triangle and mops over the bottom might be expected to damage and mutilate some starfish that were not picked up. It is therefore suggested that the starfish population is reduced by two factors simultaneously,

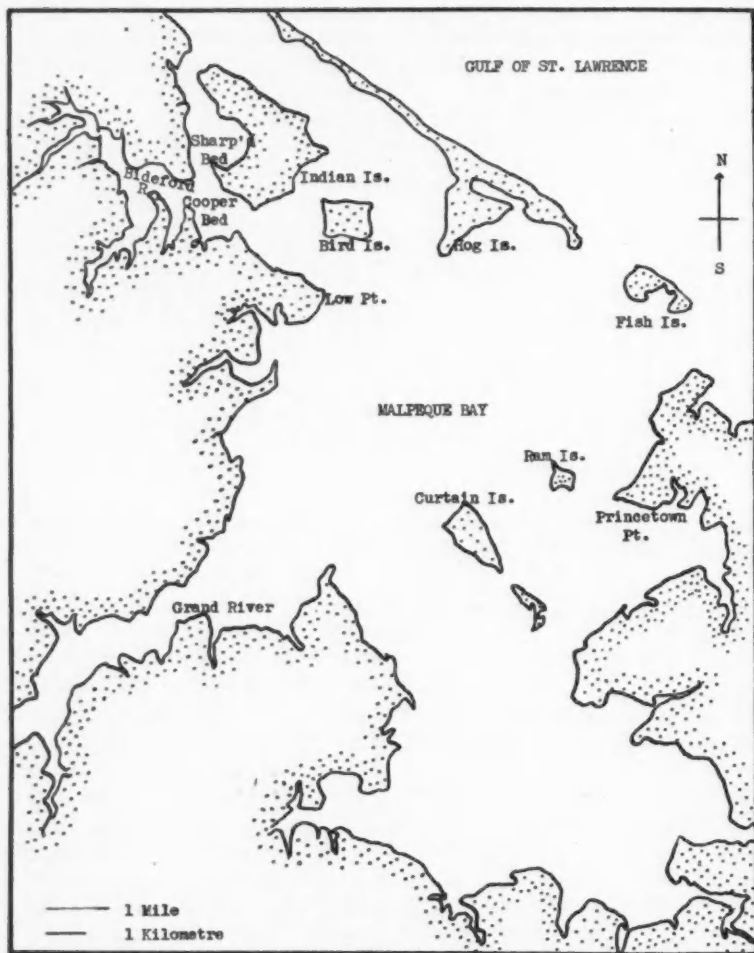


FIGURE 1. Malpeque bay.

one of which is capture by the mops and the other killing. A measure of the 'killing' at any time ( $T$ ) is therefore  $100 - K(1 - e^{-rT})$ . It must be remembered that the 'killing factor' may be the sum of several smaller factors and may be due in small degree to a mortality of the starfish from injuries from the first mopping before staining. This possibility was reduced to a minimum by only

using starfish that were apparently uninjured. It was indicated by holding apparently uninjured starfish, that had been caught by mopping and stained with Nile blue, in tanks that no significant mortality was to be expected. There would be little loss from starfish migrating off the area, as operations for recapture were begun the day after the starfish had been placed on the area and

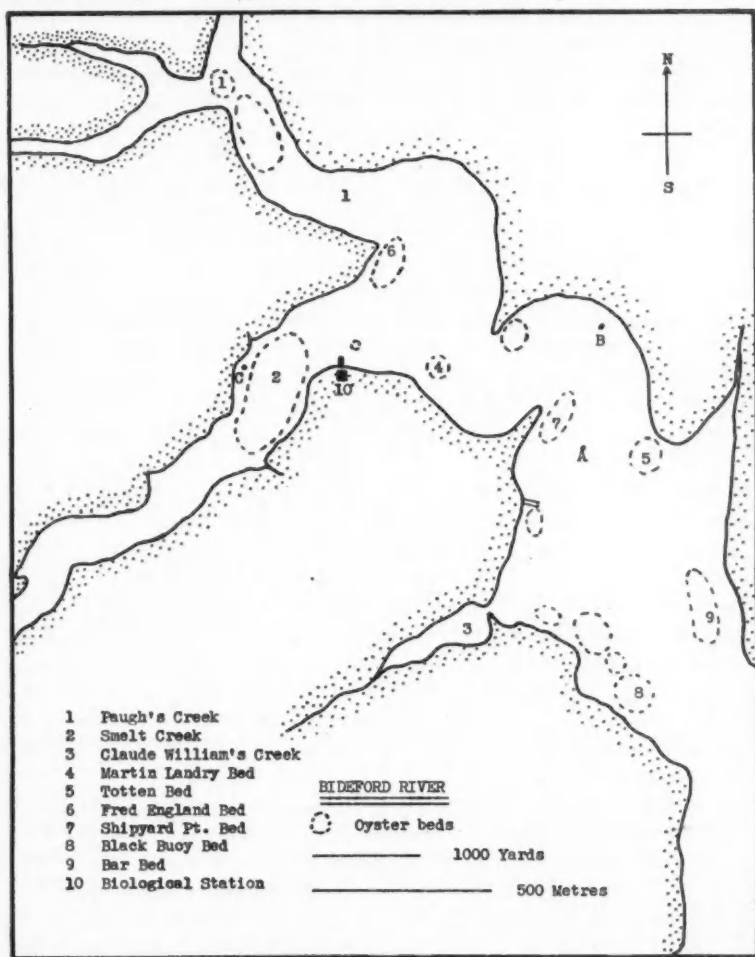


FIGURE 2. Bideford river.

experiments reported later in this paper indicate that movement is both slow and not extensive.

#### AREA INVESTIGATED

Most of the observations on starfish were carried out at the Prince Edward Island Biological Station. Bideford river, where the field work was done, is one of the arms of Malpeque bay (figure 1) and part of this area is an experi-

mental oyster reserve of the Department of Fisheries. Even in this small area there was sufficient variability of conditions to be of practical importance in starfish investigations. In a few instances observations were made in other parts of Malpeque bay. In Bideford river (figure 2), starfish were abundant except above the Biological Station in Smelt creek, in Paugh's creek and in Claude Williams' creek. Thus close to the Biological Station areas were found which did not support many starfish.

Outside of Malpeque bay, in 1936, some observations were made on starfish at the mouth of river Denys, Bras D'Or lakes, Cape Breton.

#### FACTORS LIMITING LOCAL DISTRIBUTION

In Malpeque bay the starfish were abundant on oyster areas, for the most part, except near the heads of inlets. In shallow water at the heads of inlets, the starfish were sometimes completely absent or sometimes present in small numbers. In areas not at the heads of inlets, starfish were observed in shallow water in the late spring, and, in cool weather at least, were known to invade the intertidal zone.

#### TEMPERATURE

In order to determine whether the temperature to be found in parts of Bideford river could be a factor tending to limit the distribution of starfish, experiments were performed in the laboratory. Starfish were kept in constant temperature boxes at various temperatures between 15° C. and 30° C. Starfish over 1 cm. in diameter were placed one each in an enamel-ware pan in about 800 cc. of sea water. Recently metamorphosed starfish of about 1 mm. diameter were placed in groups of five in finger bowls in about 150 cc. sea water.

A starfish was termed dead, when at the end of a three-day period, it was limp, did not cling to the dish or other support, showed no reaction with its tube feet to a needle point, and did not revive in 12 hours after being returned to room temperature.

The duration of all experiments with controlled temperature was three days, and later comparison with field results confirmed the opinion that this period was long enough to give fully significant and reliable results. In the first trials, the water was saturated with air by means of an egg-beater and the water on the starfish was changed twice a day. Control and duplicate experiments showed that both of these precautions were unnecessary, so they were discontinued. The thermostatic controls maintained the temperature with a deviation from the constant of not more than plus or minus  $\frac{1}{2}$ ° C. The normal salinity of the water in Bideford river, which was used in these experiments, was about 27 per mille.

The results (table III) show that recently metamorphosed starfish from 1 to 2 mm. in diameter survived at 27 $\frac{1}{2}$ ° C., but starfish over 9 cm. in diameter were killed at 23° C.

TABLE III. Survival of starfish of various sizes at various temperatures and various salinities (+ indicates survival through the 3-day experiment, - indicates death in less than 3 days)

Size (mm.)	At 20‰ salinity and at temperatures (°C.) as shown						At 20°C. or less and at salinities (‰) as shown			
	15	20	23	25	27½	30	15	14	13	12
1 to 2.....				+	+	-	+	+	-	-
10 to 30.....	+	+	+	+	-	-	+	+	+	-
30 to 60.....	+	+	+	+	-	-	+	+	±	-
60 to 90.....	+	+	+	-	-	-				
90 to 180.....	+	+	-	-			+	+	-	-

In addition to the laboratory experiments, starfish were placed in cages for several days near the head of Bideford river in 1934. In each case the maximum temperature was recorded by a Six's pattern maximum-minimum thermometer. Water samples were taken at low tide for salinity determinations. Table IV shows that a mortality of caged starfish occurred in the boxes where the temperature rose above 24° C.

TABLE IV. Survival of starfish placed in cages in Bideford river under varying conditions of temperature and salinity

Duration of experiment (days)	Diameter of starfish (cm.)	Maximum temperature (°C.)	Minimum salinity (‰)	Condition of starfish
6	14, 8, 5, 4, 2.	24	27.5	All alive
6	16, 8, 5, 4, 3.	24	26.1	All alive
6	13, 6, 5, 4, 3.	24½	26.3	6 cm. dead, others alive
10	8, 7, 5, 3.	26	16.0	5 cm. dead, others alive
6	12, 8, 6½, 4½, 3½	26½	16.3	4½ cm. alive, others dead
10	10, 8, 5, 3, 2½	26½	12.0	All dead
6	10, 7, 4½, 3, 3.	27	5.7	All dead

In 1935, a strip of shore near the Biological Station and quite close to the Martin Landry oyster bed was under observation, in an attempt to obtain some data on the possible shoreward migration of starfish. On August 16, two dead starfish were observed close to the shore and the temperature at the time was  $24.5^{\circ}\text{C}$ . The following day 22 dead starfish were found at the same place and the temperature was  $27^{\circ}\text{C}$ . Although the temperature was high enough to kill all the starfish, this did not occur, as apparently the temperature was not maintained at the high level for sufficient time.

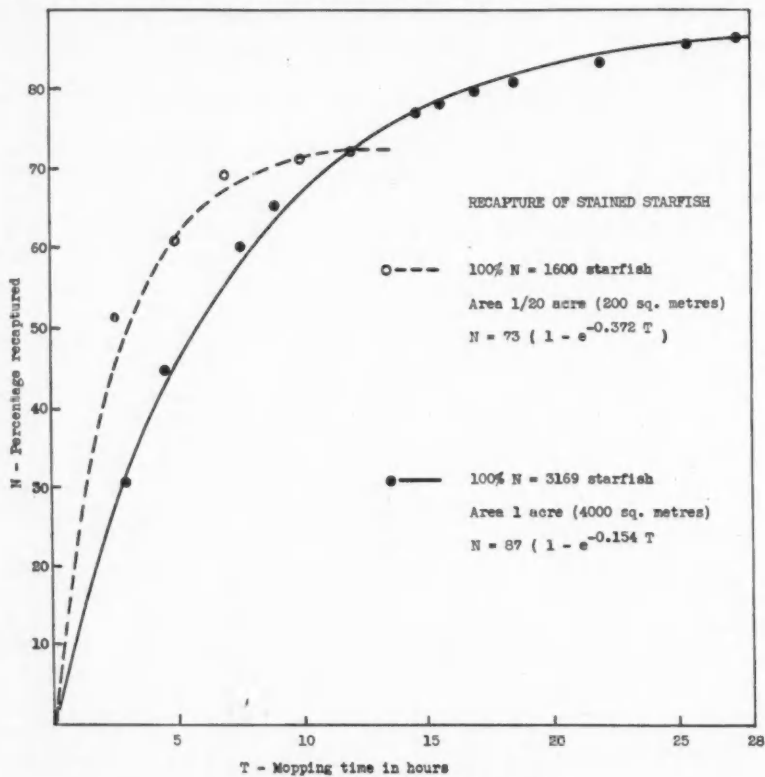


FIGURE 3. Recapture of stained starfish.

In 1936, the temperature at the Biological Station wharf did not rise above  $23.1^{\circ}\text{C}$ . and there was no evidence of starfish dying from high temperatures.

In 1937 no temperatures had been taken in Claude Williams' creek, but they would certainly have been higher (perhaps  $3$  or  $4^{\circ}\text{C}$ .) than at the Biological Station wharf, where they were recorded as above  $22^{\circ}$  on 7 different days ( $24.8^{\circ}$  on July 5) before July 15. No starfish were found in the creek on July 15, but they were present in the spring. The starfish along the shore near the Station, as observed in October, were greatly reduced in numbers, and the temperature at the wharf had been almost continuously over  $25^{\circ}\text{C}$ . during the second week in August.



The 1938 observations also indicate a mortality of starfish that can be attributed to high temperature. In June, 5,000 starfish were stained with Nile blue, but only about 5% were recaptured by mopping. Other experiments have shown (p. 85) that up to 86% of the starfish on an area can be captured by mopping, and experiments have indicated that no significant mortality of starfish was likely to be caused by staining with Nile blue. In the last part of July and the first part of August the temperature rose to 25 and 25½° C. It is believed that this temperature was the primary factor in reducing the starfish population, as was shown by the small return of stained starfish in September.

Only in 1936, of the five years in which observations were made, was there no mid-summer starfish mortality observed and only in 1936 was the temperature in the area under consideration never recorded above 23° C.

Huntsman and Sparks (1924) showed that the temperature tolerance of *Asterias forbesi* is considerably higher than that of *A. vulgaris*, when both are subjected to a standardized rate of temperature increase. *A. forbesi* is the common starfish on the oyster beds in eastern United States and the geographical ranges of the two species overlap in the northern States (Galtsoff and Loosanoff 1939).

#### SALINITY

Simultaneously with the laboratory experiments on temperature tolerance of starfish, a set of experiments was conducted to determine tolerance to reduced salinity. From the data (table III) it is seen that 14 per mille is the minimum salinity tolerated by the starfish and this figure is not specific for size as was the case in temperature toleration. Further experiments showed that starfish could withstand a salinity of 7 per mille for an hour or so if the salinity was raised to normal at the end of that time. It might be expected, therefore, that some starfish might survive a salinity of 10 or 12 per mille for the duration of one low tide, if the salinity were restored to 25 or 27 per mille when the tide rose.

In Biddeford river, no place was found where the salinity was too low for survival of starfish and at the same time the temperature not too high, at the hottest part of the summer.

Winter observations, made in February 1936, showed that starfish had either left the shallow areas to a great extent, or that starfish did not survive on the shallow areas. Under the ice, which was about two feet (60 cm.) thick, there was a layer of fresh water. With the rising and falling tide the ice also rises and falls, and therefore at low spring tides a considerable portion of the shore zone, below low tide mark, may be exposed to reduced salinity. It is believed that reduced salinity on the shore zone is responsible for the absence of starfish from this region in the winter-time.

An even clearer case of limitation of starfish distribution by salinity was found, in the summer of 1936, in the Bras D'Or lakes, Cape Breton. At the mouth of river Denys, a steep halocline was found, which was normally from one to three feet (30 to 90 cm.) from the surface. Above the halocline the water was fresh and below it about 20 per mille in salinity. The tide in the Bras D'Or

lakes is almost negligible. It was observed in June and July that starfish were not present near the mouth of river Denys although they were to be found in water 20 per mille salinity farther down the estuary. In the last part of July and in August, a set of the current year's larvae was observed below the halocline. A freshet occurred in river Denys on August 31 and the salinity from the surface to the bottom became 2.4 per mille, completely obliterating the halocline and pushing the salt water out of the river. The conditions of normal stratified water and steep halocline were not restored for two days. On examination, it was found that all the starfish had been killed by the freshet, but starfish farther down the estuary, where the salt water was not displaced, still survived.

There is a relatively extensive literature bearing on the ability of marine animals to withstand changes in the concentration or composition of the salts in the external medium. The more important papers are reviewed by Huntsman (1926), Schleiper (1930), and Dakin and Edmonds (1931). It would appear that marine animals exhibit great variation in their ability to maintain a constant salinity of the body fluids, when the external medium is changed. In general, osmotic control seems to be an active physiological process. In some cases at least, osmotic control breaks down if respiration is depressed. Henri and Lalou (1904) observed that the body fluids of echinoderms (which include starfishes) were similar to the sea water in which they lived, both in chemical composition and in concentration of the solutes. Koizuma (1932) has shown that a holothurian does not control either the concentration or composition of the body fluids and that the body fluids approximate to the concentration and composition of the external medium, even when the changes in the external medium are large. All echinoderms may be classed as strictly stenohaline, poikilosmotic, marine animals.

### FOOD

In 1935, in a brief survey of some of the bottom of Malpeque bay outside Bideford river the distribution of starfish (tables V and VI) was found to be

TABLE V. Relative abundance (numbers taken by mopping for 10-minute periods) and modal size of starfish on various types of bottom in Malpeque bay

Place	Bottom	Starfish (no.)	Modal diameter (cm.)	Place	Bottom	Starfish (no.)	Modal diameter (cm.)
Cooper bed...	oyster bed	685	2½	Bird Is. ....	sand	145	3
Sharp's bed...	" "	580	3	Low Pt. ....	"	291	3½
Curtain Is. ...	shell	475	4	Curtain Is. ...	"	68	7
" "	"	107	4	" "	mud	11	7
Ram Is. ....	"	21	3½	Indian Is. ...	"	71	3½
Hog Is. ....	rock	12	4	Princetown	"	11	7

TABLE VI. Starfish population density and modal diameter on oyster beds, as indicated by intensive mopping

Year	Bed	Number	Modal diameter (cm.)	Estimated population density	
				per a.	per sq. m.
1935	Bar	1400		1800	0.4
"	Totten	5100	6½	6000	1.5
"	Shipyard Point	5100	7	6000	1.5
"	Fred England	5500	7	7000	1.7
"	Cooper	42000	3½	60000	15.0
1937	Shipyard Point	7200	7	8500	2.1
"	Fred England	19000	7	24000	6.0
"	Totten	21500	6½	25000	6.0
"	Cooper	40000	3½	56000	14.0

by no means uniform, but on the other hand, no place was found where starfish were entirely absent. It was noticed, moreover, that the modal size of the starfish tended to be larger where the starfish were less abundant which perhaps indicates that few starfish would have more to eat per individual and become larger. Even on oyster beds where the bottom is all of much the same type, large variations in starfish population density were found and, in general, a smaller modal size of starfish where the population was dense. It is suggested under "population density" (p. 102) that in the case of starfish on oyster beds, the difference in starfish modal size and population density is due to the proximity of starfish food and food availability for starfish of different sizes. It is probable that the suitability of bottom fauna for starfish food is more important than any direct reaction of the starfish to the physical substratum on which it is found.

It was found that starfish were relatively scarce on mud bottom. This may reflect scarcity of starfish food on this type of bottom. Although mud bottom may support a large fauna, most of the forms, such as worms and clams, are buried and, as starfish do not burrow in the mud, such forms are free from attack. A similar explanation would apply to sand areas, where the sedentary, non-burrowing forms, or the slow-moving forms such as gastropods, may not be abundant enough to support or attract a large starfish population.

#### POPULATION MOVEMENT

It was mentioned above that certain small areas of bottom in Bideford river, and presumably other similar places, may be periodically, partially or wholly, denuded of their starfish population by unfavourable physical conditions. If the population is periodically reduced it must also be periodically replenished or the area will cease to support a starfish population at any time. Starfish may either invade the area as adults or may settle on the area as metamorphosing larvae after completing their free-swimming larval life. Renewal of the population takes place by both methods in Bideford river.

## SEASONAL MOVEMENT

Two shore areas, one near the Martin Landry bed and one in Paugh's creek, were under observation in 1935, in order to investigate the rate of invasion of these areas by adult starfish. In the spring, both of these areas were free from starfish, as the population of the previous fall had been driven off or killed during the winter. The invasion of the areas began to be apparent, just below low tide mark, at the end of May. The ice had completely disappeared in April and the water temperature was 15° C. The invasion of the shore zone continued at an increasing rate as the season progressed, and by June 19, 181 starfish had invaded an area of 10 sq. yd. (8.5 sq. metres) in a three day period. The temperature at that time was 20° C. The invasion continued at a diminished rate for the next 7 weeks, and during that time the daily minimum temperature was usually well over 20° C. and had risen as high as 25° C. On August 16 and 17 there was a mortality of starfish owing to the high temperature and the invasion ceased for a while. However by the end of the month, 65 new starfish were found on the area of 10 sq. yd. (8.5 sq. metres) and by September 3, 324 more.

## MOVEMENTS TOWARDS FOOD

To determine whether or not the starfish were attracted by the proximity of food in the form of living oysters, 85 of the first invaders of the Martin Landry shore area were observed closely, and placed at definite distances from a concentration of oysters. The starfish moved directly toward, but not away from, a concentration of oysters, from a distance of at least 12 metres, and the rate of such movement was approximately 6 metres per day. The starfish used in this experiment were about 4 cm. in diameter.

In an effort to see whether starfish were attracted to oysters over distances greater than 12 metres starfish were stained with Nile blue and set out on the bottom. Stained starfish were held in a floating tray for one month, with no significant mortality. It may therefore be assumed that staining with Nile blue does not seriously affect starfish. In the spring of 1936, 1,190 stained starfish were placed on the barren bottom at Station "A" (fig. 2). The closest oyster bed was 200 metres away! Three starfish were recovered on Totten bed three months later. In the meantime a few had been recovered near the point of liberation by lobster fishermen, and, on further search, a few more were recovered near the same point. The total return from this experiment was only 2%, which was considered too small to be very significant. Therefore, in 1938 the experiment was repeated. 5,000 stained starfish were placed at Stations "B" and "C" (fig. 2). 5% of the starfish were recovered in 4 months after liberation. One individual had travelled 200 metres but the average distance was only about 20 metres. There was no indication of the starfish attempting to move directly toward concentrations of oysters over long distances. The small return of starfish in this experiment is thought to be due to a mortality of starfish from temperature, which was up to 25 and 25½° C. during the four months the starfish were free.

It would appear that movements of adult starfish are quite limited, but if an abundance of food is very close at hand, that is if the stimulus is quite strong, starfish will move directly toward food. This view is further substantiated by lobster fishermen, who report that large masses of starfish collect in the lobster traps and destroy the bait.

#### DISCUSSION

Spärk (1932) reports that *A. rubens*, 100 metres from an oyster bed in Denmark, did not move to the bed, and concludes that the starfish is not attracted to food by any chemical sense. His observations agree with those in the present study, but apparently no observations could be made at distances less than 100 metres. Galtsoff and Loosanoff (1939) state that no evidence of a chemical sense could be detected in *A. forbesi*, which they kept in tanks, and that these starfish could not detect the presence of food until they came in contact with it. The observations in the present study indicate that a chemical sense is present in some degree. It is thought, however, that most of the movements of starfish are strictly random wandering, and that these movements are modified only when food is very close at hand, or when unfavourable physical conditions are encountered. Avoidance of unfavourable physical conditions would explain the smaller number of starfish that moved to the shore zone as the water was approaching the lethal temperature. There is no reason to suppose that the invasion of the shore zone is anything other than the result of random wandering, and that when in the course of such wandering some starfish stray into a zone where starfish are absent or less abundant, the result appears to be a migration into the area.

#### SPAWNING

Areas that are free from starfish may be populated by the movement of adults to the area, as discussed above, or by the settling of larvae on the area. In order to gain an understanding of this latter process, a study was made of the spawning time and the larval life of the starfish. The beginning of spawning was estimated by the examination of starfish gonads and by examination of plankton tows for larvae of the gastrula stage.

From 1935 to 1938, spawning took place mostly in the last few days in May and the first week in June. At that time the temperature is rising rapidly and varies considerably from year to year. The temperature on the average would be about 15 or 16° C. Spawning of *A. vulgaris* at St. Andrews, N.B., takes place in water that never reaches 15° C. and is usually in July. In Biddeford river, a week or so before spawning begins, most of the ovarian eggs are immature and crowded in the ovaries. Presumably, therefore, spawning takes place as soon as the sexual products are ripe, but in that area the rate of rise in temperature is greater than the rate of maturation of the sexual products and at spawning time the temperature is well above the minimal level, below which spawning could not take place. This conclusion is also suggested by the relative constancy of the date of spawning and the variability of the temperature at the time.

## SETTLING OF LARVAE

The larval life of the starfish, as estimated by peaks of abundance of larvae of the various stages in the plankton, is about three weeks in Bideford river (table VII). The gastrula, bipinnaria and brachiolaria larvae are all ciliated and planktonic.

TABLE VII. Time of maximum abundance (as shown by plankton tows) of starfish larvae in Bideford river

Year	1935	1936	1937	1938
Stage				
Gastrulae	June 5	June 4-9	May 26	
Bipinnaria	June 6-21	June 4-15	May 26-June 15	June 6-16
Brachiolaria	June 13-21	June 9-29	June 15-July 2	June 16-23

The dispersal of larvae does not appear to be a factor that limits the distribution of adult starfish in Malpeque bay. Recently settled and metamorphosed starfish have been found in the upper parts of Claude Williams' creek and Paugh's creek. This seems to be the only way that these areas are kept populated with starfish. In these places the adults are not known to survive more than one year. Owing to the higher temperature tolerance of recently metamorphosed starfish, they survive in these places where year-old starfish are killed. Although, at least in the warm water of Bideford river, most of the starfish at the end of their first year are sexually mature, the volume of sexual products shed by these small starfish (2 cm. in diameter) would not be great enough to produce a generation to succeed them. In the upper part of Paugh's creek the young starfish do not as a rule survive the winter. This is doubtless due to the larger inflow of fresh water and the presence of a slight spring freshet from melting snow. The population of starfish in upper Paugh's creek is therefore made up of individuals not more than a few months old and the population is renewed annually, not by the immigration of adult starfish, but by the settling of larvae which have come in from outside areas.

## SIZE AND RATE OF GROWTH

The modal size of the starfish obtained by mopping in Malpeque bay varies from 3 to 10 cm. depending on the locality and the season of the year.

Agassiz (1877) attempted to estimate the age of starfish found on the New England coast by counting modes in the size frequency distribution of starfish collected. Mead (1899) discounted the work of Agassiz and showed that some starfish that Agassiz called 2 or 3 years old might be only 2 or 3 months old. The numbers of starfish used by Agassiz in his age estimations were probably not large enough to be statistically significant.

There does not seem to be any way in which the age of an individual starfish can be estimated unless the conditions under which it has grown are well defined. An attempt was made to determine the age of starfish by grinding the ossicles and examining the sections under the microscope. No concentric structure in the form of rings could be found. At the same time, ossicles of sea urchins and sand dollars were similarly treated. In both of the latter, concentric rings of pigment were found. Moore (1935, 1936) published an extensive

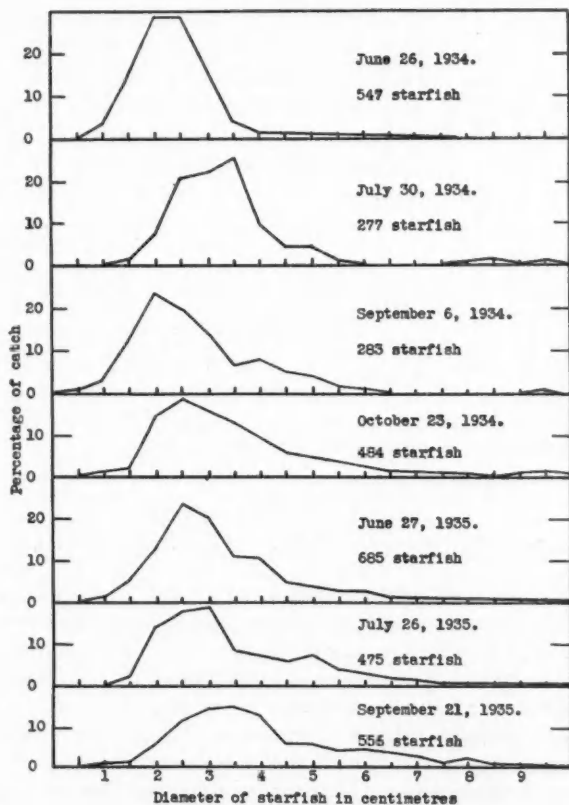


FIGURE 4. Size frequency polygons for Cooper bed starfish. Class interval,  $\frac{1}{2}$  centimetre.

study on the biology of an European sea urchin. He too observed the concentric rings in sections of the ossicles and carried the work far enough to confirm the opinion that the rings were formed annually. Although the age of an individual starfish cannot be found from any of the hard skeletal parts, an estimate of the age of individuals making up a population can be obtained from analysis of the size-frequency polygons of successive samples from the same population.



## GROWTH RATE

## FROM SIZE-FREQUENCY DISTRIBUTION

Periodic samples of the starfish populations were taken from several oyster beds in Bideford river. Figure 4 shows graphically the samples taken from Cooper bed from June 1934 to September 1935.

The mode of the size-frequency distribution for Cooper bed in June 1934 (figure 4) seems to indicate that at that time the starfish of the 1933 set, or the 0+ year class, are about  $2\frac{1}{4}$  cm. in diameter. By the end of July, the mode of the 0+ year class is about  $3\frac{1}{2}$  cm. By September the mode has become about 5 cm. for the starfish of the 1933 set which are then the 1+ year class, and the 0+ year class has made its appearance for 1934. By September 1935, the 1933 year class size-frequency distribution has become quite diffuse, and extends roughly from  $5\frac{1}{2}$  to  $8\frac{1}{2}$  cm. Thus at the end of the first year on Cooper bed, the starfish were about  $3\frac{1}{2}$  cm. in diameter, and at the end of the second year, about 6 cm. in diameter. It will be noticed that from October 1934 to

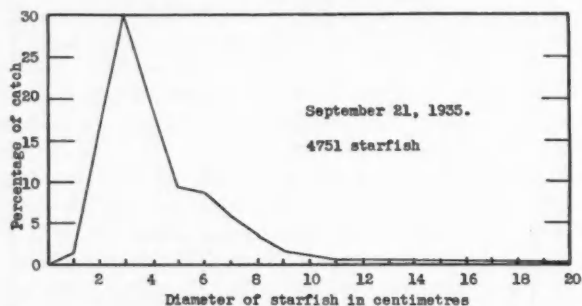


FIGURE 5. Size frequency polygon for Cooper bed starfish. Class interval, one centimetre.

June 1935 there was practically no shift in the position of the mode. This seems to indicate that starfish are almost inactive under the ice in the winter. The caging experiments showed a similar check in growth as the water became cold.

The class interval for measuring starfish was  $\frac{1}{2}$  cm. In figure 4, the distribution of sizes over 6 cm. is somewhat irregular. At first it was supposed that the irregularities showed the older age groups, but the number of starfish in these groups is small. To see whether the irregularities in the distribution were of statistical significance, a larger sample was measured on September 21, 1935. The data are plotted in figure 5. This shows that the irregularities in the smaller samples were owing to the small numbers in the samples of the larger sizes. In figure 5, the 0+ year class is below  $1\frac{1}{2}$  cm. The 1+ year class has its mode at about 3 cm. and the 2+ year class extends roughly from 5 to 9 cm. The remainder of the diagram probably represents several year classes with a maximum diameter in this sample of 19 cm. The smaller samples used in figure 4 were, however, sufficiently large to indicate the mode of the 0+ and 1+ year classes, which apparently make up the largest part of the starfish population.



Figure 6 shows successive samples from Black Buoy bed in 1934. In June the mode of the 1933 year class was about 2 cm. and the variability from about  $1\frac{1}{2}$  to  $3\frac{1}{2}$  cm. By September the mode was about  $4\frac{1}{2}$  cm. and the variability from about  $1\frac{1}{2}$  or 2 cm. to 6 cm.

In these studies the minimum size of the 0+ year class is not well marked and the starfish of the current year are not adequately sampled. This is owing to the inefficiency of the mops in capturing starfish less than about 1 cm. in diameter.

In June 1934, oyster spat of the 1933 set were planted on the Martin Landry bed. Before planting the spat, the area was cleared of starfish by intensive mopping. Experiments on the efficiency of mopping, described above, indicate

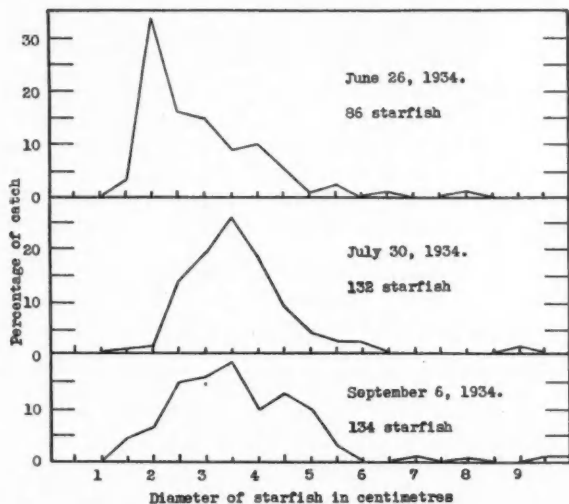


FIGURE 6. Size frequency polygons for Black Buoy bed starfish. Class interval,  $\frac{1}{2}$  centimetre.

that over 95% of the starfish on an area are killed or removed by this process. By July 23, many of the small spat were found to have been destroyed. The size frequency distribution of starfish removed from the bed on July 23 is shown in figure 7. The large size of the starfish may be attributed to rapid growth of starfish that migrated into the area, feeding on an abundance of small oyster spat. It may be argued that the immigrating population consisted only of the largest starfish from the surrounding areas. Although this is a possibility, experiments on growth (see page 100) indicate that starfish of the modal size in the surrounding populations could grow to the large size found. Thus under different conditions, starfish of the same age may vary greatly in size.

#### FROM REPEATED MEASUREMENTS

A set of experiments was carried out with starfish caged in sunken boxes and supplied with an abundance of food. The aim of the experiments was to

determine the validity of the conclusions concerning the rate of growth of starfish from size-frequency distributions of samples of populations. In each box ten measured starfish were placed with an abundance of small mussels as food. Starfish 4 cm. in diameter (table VIII) increased their diameter 43% from

TABLE VIII. Growth of starfish in cages, provided with abundance of small mussels as food. Each measurement is the average diameter of the ten starfish in the cage.

Cage	Sept. 4, 1935 Original diameter (cm.) <sup>a</sup>	Oct. 12, 1935 Increase (%)	Feb. 10, 1936 Increase (%)
1	4.2	43	
2	5.6	27	
3	6.2	25	
4	7.6	15	27
5	9.0	11	

September 4, 1935, to October 12, 1935, but starfish 9 cm. in diameter increased only 11% in the same time. Intermediate sizes increased their diameter by intermediate amounts. One box of starfish was kept under the ice and examined

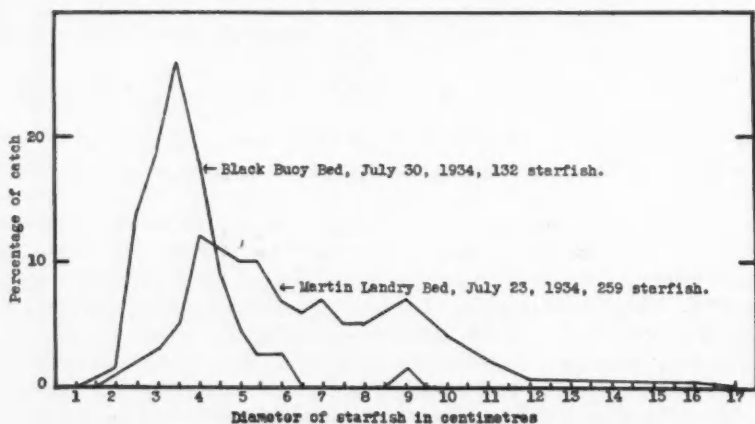


FIGURE 7. Size frequency polygons for starfish. Class interval, one centimetre.

the following February. The initial average diameter on September 4 was  $7\frac{2}{3}$  cm. The increase by October 12 was 15% and the total increase by February 10 was 27%. More growth had taken place in the first month than in the next four months.

These experiments indicate that growth rates, taken from size-frequency distributions of samples of starfish populations, are reasonable, and that the large size of the starfish on the Martin Landry bed on July 23, 1934, could be due to their rapid growth with an abundance of small food.

In measuring large starfish, care had to be taken to insure that the animal was in approximately the same state at each measurement. It was observed that a starfish 10 cm. in diameter, could contract and expand enough to make two measurements, taken within a few minutes of each other, differ by almost a centimetre. In practice the starfish were measured in an extended condition, under water in a shallow pan.

### FOOD

It was shown in the experiment reported above that with an abundance of food, small starfish could increase their diameter by 40% in a month. Mead (1899) kept starfish for several months without food and although they did not grow, they did not die. Needler (unpub. MS.) showed that a starfish must be at least one and a half times the diameter of an oyster before it can use the oyster as food, indicating that the latter must be of the proper size.

An experiment was carried out in 1938 to compare the growth of starfish using two different sources of food. Starfish of various sizes were caged, some with small mussels and some with small oysters as food. Growth (table IX)

TABLE IX. Comparative growth of starfish with mussels or oysters as food. Each measurement is the average of the ten starfish in the cage.

Food	Original diameter (cm.)	Increase in 4 mos. (%)
Oysters	5.4	35
"	7.7	13
"	10.5	4
Mussels	5.5	73
"	7.2	52

during the four months' duration of the experiment was considerably greater in the case of the starfish that were supplied with mussels as food. This experiment was by no means complete, but it indicates that variations in the rate of starfish growth, under natural conditions, may be considerably influenced by the species of animals making up the food supply. It is possible that food in the form of mussels is more easily devoured than food in the form of oysters. It is not known whether that is the explanation of the difference or whether mussel meat has greater nutritional value for the starfish than oyster meat.

## TEMPERATURE

It has been shown above (page 88) that large starfish are killed at a lower temperature than small starfish. In some places in Bidford river, such as Claude Williams' creek, the starfish that are 1+ years old do not survive the summer to become 2 years old, but starfish that are 0+ survive to become 1 year old. Considered with reference to the locality, this is a case of temperature being a factor limiting the size of starfish. On the other hand, the same case may be considered as temperature being a factor limiting the distribution of starfish above a certain size.

## POPULATION DENSITY

It has been noted above (page 92), and indicated in tables V and VI, that there is a rough inverse correlation between population density and the modal size of the starfish making up the population. This may be in part explained by theory based on consideration of the starfish population on Cooper bed, which is the most extreme example on which data are available.

It was estimated from extensive mopping of starfish on this bed, that the population density was about 60,000 starfish per acre or about 15 starfish per sq. metre and the modal diameter about  $3\frac{1}{2}$  to 4 cm. The natural reproduction of oysters on the bed is not very good, and most of the oysters are planted there, having been caught as spat elsewhere. They are, therefore, for the most part, too large to be eaten by the starfish of the modal size. In the course of random wandering, starfish that approach the area may be attracted by the large concentration of oysters. Thus a dense population may be built up and the growth may be small because most of the oysters are not available as food on account of their size. The fact that Cooper bed is almost free of mussels, may be due to the large population of small starfish which could easily devour the small mussels that set as spat on the area. Small gastropods on Cooper bed are also known to be eaten by starfish. Apparently these sources of food are not sufficient to permit much starfish growth.

## SUMMARY

The starfish, *Asterias vulgaris*, is a predator on oysters in eastern Canada.

Toward the heads of inlets and close to the shore, in Malpeque bay, P.E.I., starfish are absent or less abundant than on areas farther down the inlets or farther from shore.

It was observed that starfish over 5 cm. in diameter are killed by a continuous temperature of 25° C. but recently metamorphosed starfish, 1 or 2 mm. in diameter, survive temperatures up to 27½° C. A salinity of 14 per mille is the minimum limit for survival of all sizes. High temperature is the cause of a summer mortality and low salinity a winter mortality in shallow areas of Malpeque bay.

Populations at the heads of inlets or close to shore, that have been partially or wholly killed by unfavourable temperature or salinity conditions, are replenished by the shoreward wandering of adult starfish and the settling of larvae.

The maximum distance travelled by a stained starfish in four months was 200 metres, and the average distance, about 20 metres. They will move directly toward food for a distance of 12 metres at a rate of 6 metres per day.

Population densities of starfish on oyster beds vary from about 1,800 to 60,000 per acre (0.4 to 15 per sq. metre). Where high population densities are found the size of the individuals tends to be smaller. This may be owing to lack of sufficient food small enough to be eaten by the starfish.

The rate of growth of starfish varies with the kind and abundance of food and inversely with the size of the starfish.

Starfish in Malpeque bay spawn in the last few days in May and the first week in June. The larval life is approximately three weeks.

#### ACKNOWLEDGEMENTS

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